Decomposition driven by invertebrates in tropical rice ecosystems: impacts of management strategies

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(Altes Sprichwort)

Batad Rice Terraces, Philippines | Foto: M. Schädler

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LIST OF ARTICLES

This thesis is based on the following publications and manuscripts. The author's and co-authors' contributions are listed below.

Article I

"Small-scale variability in the contribution of invertebrates to litter decomposition in tropical rice fields"

Schmidt, A., H. Auge, R. Brandl, K. L. Heong, S. Hotes, J. Settele, S. Villareal, and M. Schädler (2015). DOI: 10.1016/j.baae.2015.01.006. *Basic and Applied Ecology.*

The study was designed by M. Schädler, R. Brandl, H. Auge and me. I did the field work, analyzed the data and wrote the manuscript. All co-authors commented on earlier versions of the manuscript.

Article II

"Effects of residue management on decomposition in irrigated rice fields are not related to changes in the decomposer community"

Schmidt, A., K. John, G. Arida, H. Auge, R. Brandl, F. G. Horgan, S. Hotes, L. Marques, N. Radermacher, J. Settele, V. Wolters, and M. Schädler (2015). DOI: 10.1371/journal.pone.0134402. *PLOS ONE.*

The study was designed by M. Schädler, R. Brandl, H. Auge and me. I did the field and laboratory work with the help of K. John and N. Radermacher. I conducted the data analyses and wrote the manuscript. All co-authors commented on earlier versions of the manuscript.

Article III

"Compensatory mechanisms of litter decomposition under alternating moisture regimes in tropical rice fields"

Schmidt, A.*, K. John*, H. Auge, R. Brandl, F. G. Horgan, J. Settele, V. Wolters, A. S. Zaitsev, and M. Schädler (to be subm.). *Applied Soil Ecology.* (* shared first-authorship)

The experiment was designed by M. Schädler, R. Brandl, H. Auge, K. John and me. Field and laboratory work was conducted by K. John and me. I performed the data analyses. The manuscript was written by me with the help of K. John. All co-authors commented on earlier versions of the manuscript.

Article IV

“Rice straw consumption by the invasive apple snail *Pomacea canaliculata* (Caenogastropoda, Ampullariidae)”

Türke, M.*, **A. Schmidt***, M. Schädler, S. Hotes, and W. W. Weisser (under review). *Malacologia*. (* shared first-authorship)

The study was designed by M. Türke and me. The experiment was conducted by M. Türke. The data was analyzed and the manuscript was written by M. Türke and me. All co-authors commented on earlier versions of the manuscript.

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Zusammenfassung

Für über ein Drittel der Weltbevölkerung stellt Reis das wichtigste Grundnahrungsmittel dar. In Asien hat der bewässerte Reisanbau eine Jahrtausende lange Tradition und ist bis heute ein wichtiger Bestandteil der asiatischen Kultur. Aufgrund des exponentiellen Bevölkerungswachstums, vor allem in Süd-Ost-Asien, wurde in den letzten Jahrzehnten nach immer neuen Möglichkeiten zur Steigerung der Ernteerträge gesucht. Es wurden neue ertragreichere Reissorten gezüchtet, große Landschaftsflächen zu Reis-Monokulturen umgewandelt und effektivere Düngemittel sowie Breitband-Pestizide entwickelt. Die neuen Reissorten benötigten allerdings deutlich mehr Düngemittel, was nicht nur eine hohe finanzielle Belastung für die Bauern darstellte, sondern auch die Anfälligkeit der Reispflanzen für bestimmte Krankheiten/ Infekte erhöhte. Veränderungen der lokalen Fauna-Gemeinschaften führten unter anderem zu einer verminderten Effektivität der natürlichen Schädlingskontroll-Mechanismen. Der daraus folgende Anstieg des Schädlingsbefalls und die damit einhergehenden stetig zunehmenden Ernteverluste haben dazu beigetragen, dass sich das Interesse verstärkt auf alternative Möglichkeiten für einen nachhaltigen Anbau und auf die Bewahrung der natürlichen Ökosystemdienstleistungen in der Reislandwirtschaft verlagerte.

Für eine nachhaltige und natürliche Steigerung der Bodenfruchtbarkeit ist Reisstroh die potenziell wichtigste Nährstoffquelle in Reisfeldern. Um den Stickstoff im Stroh effektiv freisetzen zu können, ist eine funktionierende Gemeinschaft von Bodenorganismen unerlässlich. Unter den anaeroben Bedingungen der Reisfeldböden, die während der Anbauphase permanent gefluteten sind, spielen Invertebraten für die Zersetzung von organischem Material eine besonders wichtige Rolle. Das generelle Ziel unserer Experimente war daher, die Zusammensetzung der Fauna-Gemeinschaft in Reisfeldern im Zusammenhang mit ihrem Beitrag zum Abbau von Reisstroh zu untersuchen. Um den mikrobiellen Abbau von dem der Zersetzer-Fauna zu differenzieren, wurden Streubeutel mit zwei verschiedenen Maschenweiten (20 µm und 5 mm) verwendet und entweder auf die Bodenoberfläche der Reisfelder gelegt oder in die oberste Bodenschicht eingebracht. Bodenkern-Proben wurden zur Bestimmung der Bodenfauna verwendet und Wasserkescher-Proben zur Erfassung der aquatischen Fauna.

Die Ergebnisse unserer ersten Studie zeigen deutlich, dass Invertebraten einen großen Einfluss auf die Zersetzung von Reisstroh haben und damit die Bodenfruchtbarkeit positiv beeinflussen können. Einige Zersetzer-Arten leben nur als Larven im Wasser bzw. den gefluteten Böden und benötigen als Adulte eine ausreichende Strukturvielfalt in der Umgebung der Felder. Wir konnten zeigen, dass in Ufernähe die Abbauaktivität der Fauna am höchsten ist und Richtung Feldmitte stetig abnimmt. Anstatt ein großes Reisfeld anzulegen, könnte das Aufspalten der

Fläche in mehrere kleine Felder die Nährstofffreisetzung durch den Abbau von Reisstroh fördern und zur Verbesserung des Pflanzenwachstums beitragen.

Das Ziel unserer zweiten Studie war es, den Einfluss verschiedener Bewirtschaftungsformen, genauer, den unterschiedlichen Umgang mit Ernterückständen auf die Aktivität der Zersetzer-Invertebraten und die Abundanzen der Wasser- und Bodenfauna zu untersuchen. Im Gegensatz zur Düngung mit der Asche von verbranntem Stroh, konnten in den Feldern, in denen Reisstroh als natürlicher Dünger verwendet wurde, eine deutlich höhere Anzahl an wirbellosen Tieren erfasst werden. Auch die Menge an abgebautem Stroh war stark abhängig von der jeweiligen Form der Bewirtschaftung. Generell konnte kein Zusammenhang zwischen der Abundanz der Boden- und Wasserfauna und der Abbaugeschwindigkeit des Reisstrohs in unseren Streubeuteln festgestellt werden. Dennoch konnten wir nachweisen, dass das Einbringen von Reisstroh in Reisfelder sowohl einen signifikanten Einfluss auf die Abbaugeschwindigkeit durch die Zersetzer-Fauna hat, als auch die Abundanz diverser Faunagruppen deutlich erhöhen kann. Um einen genaueren Einblick in die Zersetzungsvorgänge und den jeweiligen Beitrag der Fauna und der Mikroorganismen in Reisökosystemen zu bekommen, sind Langzeitstudien über mehrere Anbauperioden nötig. In dieser Zeit könnte sich die Gemeinschaft der Bodenorganismen an die veränderten Bewirtschaftungspraktiken anpassen.

Die Einführung einer Trockenanbau-Periode im Wechsel mit Nassreis kann dazu beitragen, den enormen Wasserverbrauch und die extrem hohen Mengen an Treibhausgasen, die der geflutete Reisanbau produziert, zu reduzieren. Solch ein Fruchtwechsel birgt natürlich auch Risiken, besonders für die Gemeinschaft der Bodenorganismen. Deshalb haben wir verschiedene Fruchtwechsel daraufhin untersucht, welchen Einfluss sie auf die Abundanz und Aktivität der Bodenfauna haben. Mikrobielle Abbauprozesse sind bekanntermaßen unter Sauerstoffmangel stark verlangsamt. Daher war der mikrobielle Abbau des Reisstrohs unter den aeroben Bedingungen der Trockenphase sehr stark erhöht. Obwohl wir eine sehr viel höhere Anzahl an Invertebraten im Boden der Trockenfelder nachweisen konnten, war der Beitrag der Bodenfauna zum Streuabbau in dieser Zeit vernachlässigbar. Nach dem Fruchtwechsel zu geflutetem Nassreis zeigte die Zersetzer-Fauna wieder eine sehr hohe Aktivität, während der mikrobielle Beitrag stark abnahm. Der Gesamtverlust an Stroh unterschied sich am Ende zwischen den Fruchtwechseln nicht. Das heißt, die Gemeinschaft der Bodentiere ist in der Lage den stark verlangsamten mikrobiellen Abbau im gefluteten Nassreis-Anbau zu komplementieren, was sie zu einem essentiellen Faktor für die nachhaltige Verbesserung der Bodenfruchtbarkeit macht.

Die Goldene Apfelschnecke (*Pomacea canaliculata* L.) ist eine der häufigsten Reisschädlinge, allerdings nur am Anfang der Anbauphase, wenn die Reispflanzen noch sehr klein sind. Wir wollten daher untersuchen, ob solche mutmaßlich ausschließlichen Schädlingsorganismen auch positive Einflüsse auf das Ökosystem und den Nährstoffhaushalt des Bodens haben können. In einem Laborexperiment konnten wir zeigen, dass sich Apfelschnecken alternativ auch von Reisstroh ernähren und damit die Zersetzungsraten sowie den Nährstoffhaushalt in gefluteten Reisfeldböden steigern könnten, sobald die Reispflanzen nicht mehr anfällig für Schneckenfraß sind.

Generell ist die Zersetzer-Fauna ein entscheidender Faktor auf dem Weg hin zu mehr Nachhaltigkeit im bewässerten Reisanbau. Sie kompensiert den stark eingeschränkten mikrobiellen Abbau von organischem Material unter den vorherrschenden anaeroben Bedingungen und beeinflusst damit die Versorgung des Bodens mit wichtigen Nährstoffen. Eine stabile Gemeinschaft von Bodenorganismen ist ausschlaggebend für ein optimales Pflanzenwachstum und kann dazu beitragen, die Bodenfruchtbarkeit zu steigern und dadurch den Bedarf an künstlichen Düngemitteln zu reduzieren. Es sollte daher genau untersucht werden, welche Auswirkungen sowohl landwirtschaftliche Intensivierungsmaßnahmen und der damit einhergehende Verlust an Biodiversität als auch der Klima- und Landnutzungswandel auf die Gemeinschaft und Funktionalität der Bodenorganismen haben.

Chapter 1

GENERAL INTRODUCTION

RICE AGRICULTURE

History and current problems

Irrigated rice cultivation is one of the oldest and most important agricultural branches in Asia (Kurihara 1989). Its history dates back around 9000 years and is assumed to have originated in Northeast Thailand (Bray 1994). Almost ⅓ of the world's population lives in Asia where the staple diet mainly consists of rice (*Oryza sativa* L.) and where more than 90 % of global rice yields are produced (FAO 2007, USDA 2007). With an estimated increase of the human population up to 9.6 billion people by 2050 (acc. E/CN.9/2014/3, United Nations) the demand for an improved food productivity continuously increases. Under the pressure of an increase in rural poverty along with permanent food shortages from the mid-1960s onwards a 'package' of improvements for rice cultivation was introduced officially promoted by local extension services and credit schemes (Bray 1979). The initiatives, known as "*The Green Revolution*", were firstly introduced to India and soon got adapted by farmers all over the world, particularly in developing countries (Gaud 1968). Due to the introduction of new high-yielding and fast-growing varieties as well as an intensified use of fertilizers, herbicides and pesticides the global rice yield per year increased from 364 million tons to 473 million tons within one decade (Fernando 1993). New hybrid rice varieties started to take over from conventional (= inbred) varieties (Horgan and Crisol 2013). However, shortly after their introduction farmers reported an increasing frequency and intensity of insect pests and diseases (Horgan and Crisol 2013). Compared to conventional varieties hybrid rice requires much higher input of fertilizers to reach its full yield potential (Van Pham et al. 2003, Kumar and Prasad 2004). However, an increasing use of fertilizer is often linked to higher levels of rice plant damage caused by certain pest species (Cheng 1971, Visarto et al. 2001, Jiang and Cheng 2003, Lu et al. 2004, Horgan and Crisol 2013). This, in turn, brought farmers to increase the usage of new and highly effective pesticides concurrently resulting in a reduction of natural pest control mechanisms regulating the abundance of rice herbivores (Kenmore et al. 1984, Reissig 1985, Horgan and Crisol 2013). At the same time, whole regions with formerly high structural landscape diversity got transformed into contiguous areas of rice monocultures (Bambaradeniya and Amarasinghe 2003). The overuse of fertilizers and pesticides together with this conversion of landscapes resulted in a rapid boom of rice pests and diseases (Thresh 1989, Bottrell and Schoenly 2012). The re-establishment of a functioning rice field community is necessary for the efficient natural regulation of pest populations. Studies on the faunal community and their complex food web structures are therefore an essential part for the integration of sustainable agricultural practices preventing regular pest outbreaks.

Besides, flooded rice agriculture, in particular irrigated rice cropping, requires an extremely high amount of water and is a major source of atmospheric methane (Houghton 1995, Reicosky et al. 2000, Wassmann et al. 2000b). Therefore, one of the main objectives in current rice research is the stabilization of greenhouse gas concentrations in the atmosphere at a level that does not harm the environment while ensuring sufficient rice productivity for a steadily increasing population (Wassmann et al. 2000a, Wassmann et al. 2000b).

Cultivation

The following description refers to the cultivation of the semi-aquatic rice plant *Oryza sativa* L. (also called “Asian rice”) in irrigated lowland fields (“paddy fields”). Alternative cultivation methods include deep water rice (floating rice), upland rice (dry cropping), rainfed upland rice and rainfed lowland rice.

In Southeast Asia irrigated rice cultivation typically comprises two to three crop cycles per year. Field preparation in the fallow period includes plowing, harrowing and land leveling. Seeds are either directly sown (direct seeding) or cultivated in dry or wet nursery seedbeds before the seedlings are transplanted into the fields (Nwilene et al. 2008, pers. observation). The application of pesticides (e.g. insecticides, molluscicides, herbicides) and artificial fertilizers is common practice throughout the cropping period. Around 70 to 90 days after transplanting rice plants are harvested, threshed and dried (Nwilene et al. 2008, pers. observation). Rice straw residuals are either burned directly on the fields, applied as organic fertilizer for the next cropping season or used as fodder (Singh et al. 2005). Typically, soils are continuously flooded during the cropping season and fall dry periodically during the fallow phases. The different stages of rice plant growing are shown in Figure 1.

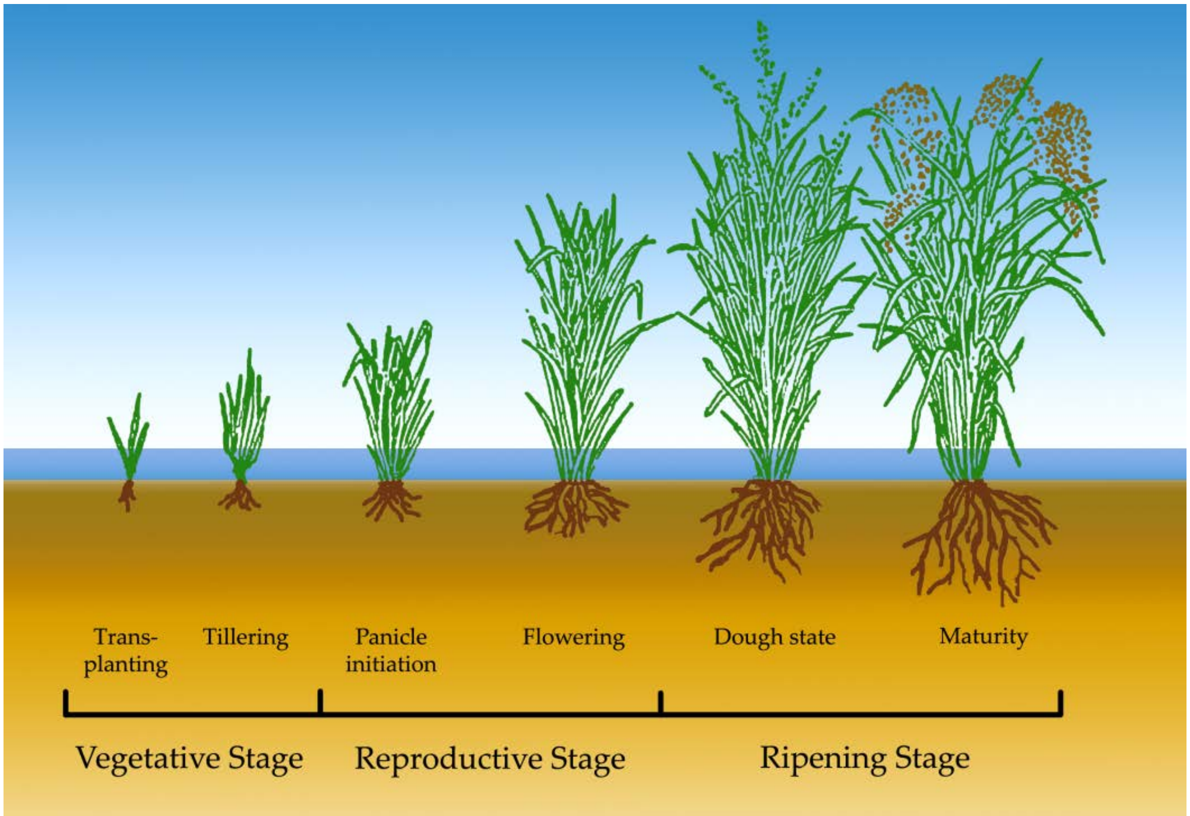

Figure 1 Growing stages of a rice plant (*Oryza sativa* L.).

DECOMPOSITION PROCESSES

Decomposition of organic matter is a fundamental ecosystem process regulating energy flow and nutrient cycling, thereby influencing plant growth as well as community dynamics and structures (e.g. Swift et al. 1979, Wardle 2002, Gartner and Cardon 2004, Bardgett 2005). In broad terms, decomposition describes the transformation of organic matter through physical (e.g. fragmentation, leaching), chemical (e.g. oxidation, condensation) and biological (e.g. digestion, enzymatic processes) mechanisms (Berg and McClaugherty 2008). In the beginning of the decay process easily soluble organic compounds are liberated by leaching. Further, fragmentation of the plant material by macro- and meso-detritivores increases the surface area extending microbial colonization (Heath et al. 1964). By enzymatic degradation microorganisms break down the organic compounds of the plant detritus into its basic components (Wolters 1991). Under aerobic conditions microbial decomposition leads to a release of CO_2, while with limited oxygen availability decomposition mainly produces organic acids (Berg and McClaugherty 2008). Anaerobic mineralization processes also yield several inorganic compounds, e.g. NH_4^+, PO_4^{2-}, NO_2^- or NO_3^- (Swift et al. 1979).

The rate of decomposition is influenced by a variety of interacting biotic and abiotic factors (Villegas-Pangga et al. 2000, García-Palacios et al. 2013) including the chemical composition of organic matter (C/N ratios, lignin concentration etc.), environmental conditions (temperature, soil moisture content, pH etc.) and management factors in agricultural fields, like tillage or pesticide application (Bollen 1953, Tian et al. 1993, Singh et al. 2005). For example, high clay contents in the soil or high lignin concentrations in the litter were shown to decelerate the decay process (Jenkinson 1977, Merckx et al. 1985, Tian et al. 1992, Singh et al. 2005). In agricultural systems crop residues, like straw are valuable materials for site fertility (Mary et al. 1996, Bhogal et al. 1997, Singh et al. 2004). Despite the importance of rice for food security, decomposition of rice straw residuals as important natural nutrient source in wet rice agriculture attracted little attention in rice research. Hence, studies on the decomposition processes and dynamics as well as on factors influencing decay rates are still rather rare.

RICE FIELD FAUNA

Flooded rice agriculture creates a special ecosystem with regular changes in water availability between cultivation and fallow periods causing periodic shifts in soil aeration from anaerobic to aerobic conditions (Bambaradeniya and Amarasinghe 2003). Hence, the faunal assemblage of paddy fields is adapted to such drastic environmental changes. There are many studies that investigated animal groups in rice fields focusing on the aboveground, or better on the 'above-water' community. The major part of this research comprised rice pest species (Kiritani 1992, Settele 1992, Cohen et al. 1994) or their predators and parasitoids as important natural pest control agents (Kenmore et al. 1984, Reissig 1985, Schoenly et al. 1996, Ives and Settle 1997, Drechsler and Settele 2001). The most common and widely studied rice herbivores include: brown planthopper (BPH, *Nilaparvata lugens* Stal), whitebacked planthopper (WBPH, *Sogatella furcifera* Horvath); green leafhopper (GLH, *Nephotettix malayanus* Ishihara & Kawase and *Nephotettix virescens* Distant) and different species of stem borers, like the white stem borer (WSB, *Scirpophaga innotata* Walker). Most common predators in rice fields are spiders (e.g. *Tetragnatha sp.*), beetles (e.g. *Micraspis discolor* Fabricius) and odonates (e.g. *Agriocnemis pygmaea* Rambur; Bhattacharyya et al. 2006, Rattanapun 2012). Parasitoids comprise species of several families of hymenopterans, e.g. *Mymaridae*, *Ichneumonidae* and *Trichogrammatidae* which have a wide range of herbivore hosts (Gurr et al. 2011, Gurr et al. 2012). Though, a permanent overuse of pesticides, especially insecticides decreases the abundance and efficiency of these natural pest control agents which can result in inevitable pest outbreaks (Bottrell and Schoenly 2012, Horgan and Crisol 2013).

Studies, which focused on aquatic or soil-dwelling faunal groups, have shown that flooded rice fields harbor the whole spectrum of freshwater fauna (Fernando 1977, 1993). The most widely studied groups of aquatic organisms are taxa of zooplankton, mainly rotifers (Fernando 1979, Bambaradeniya and Amarasinghe 2003). Around 50 % of the invertebrate species are arthropods which mostly comprise insects. Most insects are aquatic larvae belonging to the dipteran families *Culicidae* (Mosquitoes; Bambaradeniya 2000) and *Chironomidae* (nonbiting midges; Bambaradeniya and Amarasinghe 2003). Invertebrate groups, which are involved in the decay of organic matter in paddy fields, comprise semi-terrestrial forms of oligochaete worms, like *Enchytraeidae* or *Naididae* as well as aquatic chironomid larvae, nematodes and microcrustaceans (e.g. Weerakoon and Samarasinghe 1957, Kurihara 1989, Simpson et al. 1993a, b, Bambaradeniya and Amarasinghe 2003). Soil-dwelling micro-arthropod decomposers, like *Acari* or *Collembola* show comparatively low abundances and are therefore of limited importance for the decomposition process in flooded rice fields (Cancela da Fonseca and Sarkar 1998, Widyastuti 2002, Liang et al. 2005). Figure 2 gives an overview of aquatic and edaphic invertebrate groups which are typically involved in the decomposition process of organic matter in tropical rice fields.

Apart from their relevance in the decay of organic material, decomposer invertebrates may also play a crucial role for natural pest control. Among the most important pest control agents are generalist predators feeding on rice herbivores (Settle et al. 1996). However, early in the rice cycle rice herbivores, especially arthropods are relatively low in abundance and therefore not a sufficient food source for their natural enemies. Settle et al. (1996) theorized that during these periods invertebrate decomposers could constitute an alternative food source for generalist predators. Promoting the population size of these predatory species throughout the year could maximize natural pest control by suppressing pest populations below an economic threshold level.

This approach is also supported by the IPM concept (integrated pest management, Heong et al. 1991) which gained increasing popularity among rice field farmers in the recent years. It aims at enhancing the sustainability in rice agriculture by minimizing the use of pesticides and fertilizers while maintaining pest control as well as crop productivity (Knipling 1972). Attempts to implement the IPM approach in rice agriculture also increased the awareness for the importance of aquatic and below-ground faunal groups. Nevertheless, the structure of the decomposer community as well as factors which might influence their abundance and activity are still hardly understood.

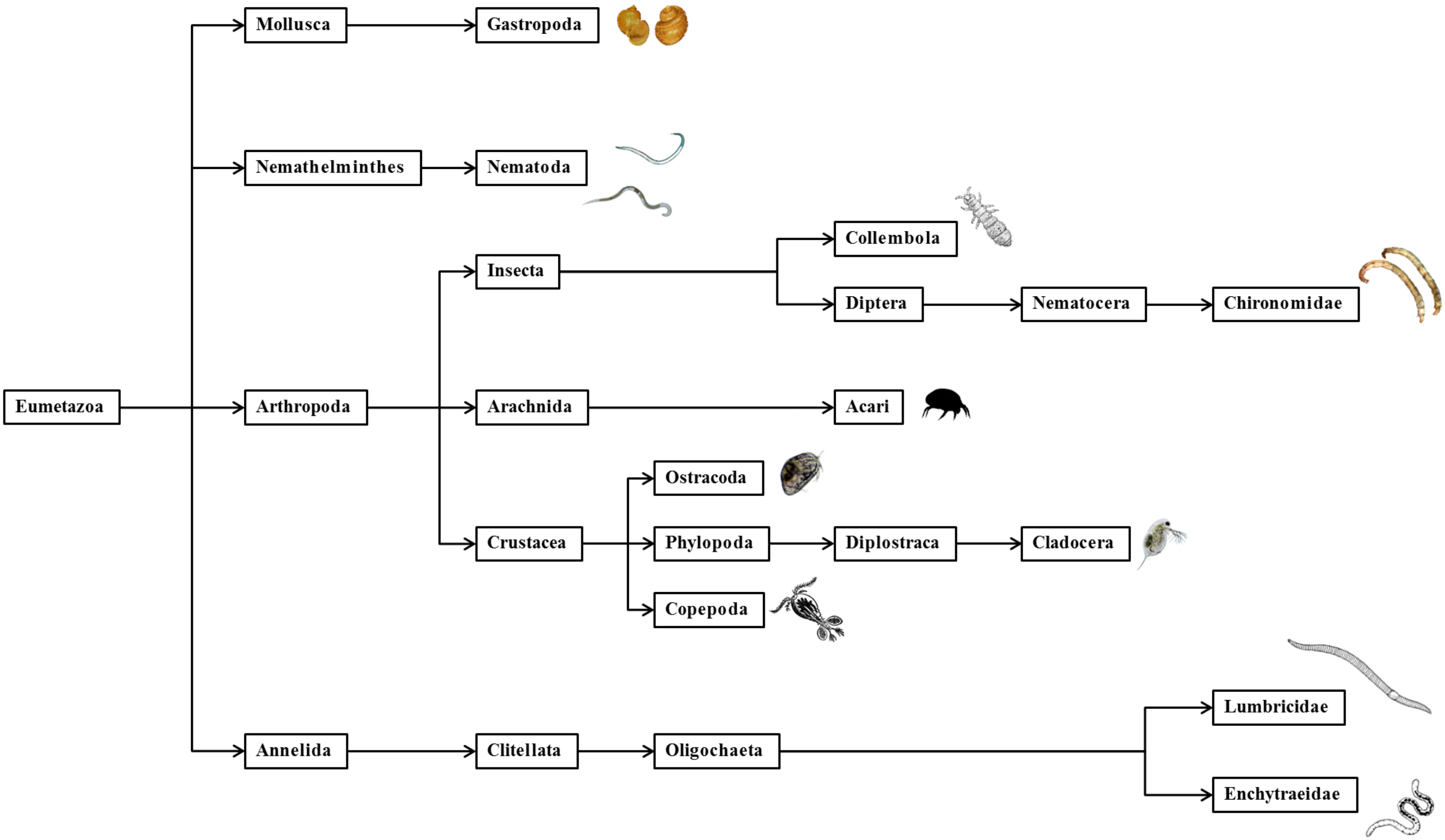

Figure 2 Phylogenetic tree (following Storch and Welsch 1991, Gruner 1993, Klausnitzer 2003) of the most important invertebrate groups involved in the decomposition process in tropical rice fields.

IMPACT OF FIELD MANAGEMENT ON DETRITIVORES

- CURRENT STATE OF KNOWLEDGE -

Decomposition of organic matter is an essential part for the integration of sustainable management practices in agroecosystems and highly dependent on a stable and functioning decomposer community (Beare et al. 1997, Ferreira et al. 2012). The complex interactions between microbes (fungi, bacteria) and invertebrate decomposers trigger the efficient breakdown of nutrients bound in dead organic material (Anderson 1988, Wolters 1991, Lavelle et al. 1994, Powell et al. 2014). The activity of invertebrate decomposers as well as of microorganisms primarily depends on moisture and temperature (Kowalenko et al. 1978, Heal et al. 1997, Villegas-Pangga et al. 2000, Singh et al. 2005, Riutta et al. 2012). During the process of litter decomposition soil invertebrates often have rather indirect effects on the release of nutrients (Witkamp and Ausmus 1976, Tian et al. 1993, Khandaker et al. 2004, Schmidt et al. 2015a). For example, by increasing the litter-soil contact through the fragmentation of plant materials invertebrate decomposers create a more stable and favorable micro-environment for microbial decomposition (Lekha et al. 1989, Singh et al. 2005). Generally, decomposer organisms prefer high quality substrates with low C/N ratios and low lignin contents (Canhoto and Graça 1995, Swan and Palmer 2006, Ferreira et al. 2012). For the decomposition of low-quality litter (like rice straw) the role of soil invertebrates is relatively greater as high C/N ratios and high contents of lignin and polyphenol decrease the decomposability of organic matter for microorganisms (Tian et al. 1995). In soils of flooded rice fields the anaerobic conditions cause an additional deceleration of microbial decomposition rates (Koegel-Knabner et al. 2010). Therefore, especially in wet rice agriculture invertebrate decomposers significantly accelerate the decay of crop residues (Santos and Whitford 1981, Reddy et al. 1994, Schmidt et al. 2015b). Hence, they are assumed to be an essential component in soil cycling processes (Lekha et al. 1989, Widyastuti 2002) and of high importance for enhancing and maintaining soil productivity and quality (Tian et al. 1993, Chaudhury et al. 2005).

Anthropogenic activities, like crop residue and pest management practices affect the structure and composition of the entire faunal community in rice agroecosystems including the density and activity of decomposer organisms (Heong et al. 1991). For example, high tillage intensity has been shown to be associated with a decline in invertebrate abundance which decreased the rate of straw decomposition (Friebe and Henke 1991). The use of rice straw residuals as organic fertilizer in paddy fields was shown to have positive effects on soil faunal abundances (Singh et al. 2005, Schmidt et al. 2015b). Besides, landscape transformation into structurally poor rice monocultures can have negative effects on the decomposer community, especially on semi-aquatic invertebrates with aquatic larval and terrestrial adult stages which depend on a certain level of landscape diversity near to paddy fields (Schmidt et al. 2015a). The structure of the decomposer community may also be altered by invasive species, like Golden Apple Snails (*Pomacea canaliculata* L.). Golden Apple Snails are known to feed on freshly transplanted rice seedlings (Estebenet 1995) and therefore they are one of the most damaging pest species in the early stages of rice growing (Cowie 2002). Nevertheless, after few weeks when rice plants become unpalatable for the snails (Litsinger and Estano 1993) they must switch to other food resources which could include rice straw litter in the field.

Up till now, the role of invertebrate decomposers in the process of rice straw decomposition in flooded paddy fields is hardly understood (Settle et al. 1996, Schmidt et al. 2015a). However, for an integration of sustainable soil productivity it is important to investigate the complex interactions within the decomposer network (Anderson 1988, Lekha et al. 1989, Heong et al. 1991, Wolters 1991, Lavelle et al. 1994, García-Palacios et al. 2013) which comprise macro- and meso-decomposers (invertebrates) as well as micro-decomposers (fungi, bacteria). Even though some researchers examined groups of aquatic or below-ground animals or the decomposition of rice straw (e.g. Fernando 1977, Bambaradeniya and Amarasinghe 2003), there is still a lack of studies/ experiments which elucidate the **connections** and **interactions** between (a) aquatic and (b) soil-dwelling **decomposer invertebrates**, (c) their influence on the **decay of rice straw** residuals and further, (d) the impact of agricultural intensification and **management practices** on their community structure and decomposition activity in paddy fields.

THE LEGATO-PROJECT

This thesis is based on studies and experiments which were conducted within the framework of the international and interdisciplinary project “LEGATO”. LEGATO stands for: **L**and-use intensity and **E**cological En**G**ineering **– A**ssessment **T**ools for risks and **O**pportunities in irrigated rice based production systems (Settele et al. 2015). The project involves different partners from Southeast Asia (Philippines, Vietnam and Malaysia) and Europe (Germany, Scotland, Bulgaria and Spain). In the light of changes in land use intensity, climate and biodiversity LEGATO aims at analyzing the potential of ecological engineering for supporting rice crop productivity along with improving pest control, methods of sustainable land management, crop related biocontrol as well as socio-economic and cultural applications. A main objective of LEGATO is the implementation of different observational and experimental studies on the contribution of a preserved biodiversity for the integration of ecosystem functions and services. Research in LEGATO is conducted in seven regions in Southeast Asia, four in Vietnam and three in the Philippines, which include landscapes along a gradient of changing geology, climate, land use intensity, agricultural practice and cultural conditions (Klotzbücher et al. 2015, Settele et al. 2015). My field studies were carried out either directly on LEGATO fields or on special experimental sites in two regions located in the lowlands of Luzon Island in the Philippines. Nueva Ecija is a province in the middle of Luzon (elevation: 50 m above sea level; latitude 15.67, longitude 120.89 WGS84 decimal degrees) which reflects a rice dominated landscape with highly intensive rice agriculture and low structural diversity. In contrast, the rice fields in the Laguna province in the south of Luzon (elevation: 200 m above sea level; latitude 14.2, longitude 121.4 WGS84 decimal degrees) are embedded in a diverse landscape structure with less intensive land use activities (for a detailed description of topography, geology, soil conditions and climate see Klotzbücher et al. 2015). Since invertebrate decomposers are potential key organisms triggering the dynamics of nutrient turnover with consequences for site fertility, my studies aimed at investigating their role in the decomposition process in rice fields and the factors which mediate these processes.

RESEARCH OBJECTIVES AND THESIS OUTLINE

The ultimate aim of this thesis is to assess the role of decomposer organisms as an essential part for the development and integration of management practices for sustainable soil productivity. My research focused on decomposer organisms in the soil and aquatic phase of flooded rice fields. I was particularly interested in the contribution of decomposer invertebrates to rice straw decomposition and how different agricultural management practices as well as biotic and abiotic changes in their environment might influence their activity and efficiency along with possible alterations of their assemblage. The studies presented in this thesis address topics that might help to increase our understanding of the decomposition dynamics in rice-based ecosystems and the relevance of invertebrates for nutrient cycling processes. The Chapters 2, 3 and 4 of this thesis describe field experiments carried out in the Philippines; the 5th Chapter presents a laboratory experiment conducted in Germany.

Chapter 2 describes a decomposition experiment in unmodified rice fields managed by local farmers. Within the aquatic phase we measured rates of rice straw decomposition in dependence on the distance to the field border. Many meso- and macro-decomposers are aquatic organisms during their larval stages, but terrestrial and dependent on suitable vegetation structures during their adult stage. I therefore chose fields with different surrounding vegetation structures and hypothesized that rice straw decomposition by invertebrates decreases with increasing distance to these structures.

The assemblages and abundances of animal groups in rice fields are likely to be influenced by management practices of crop residues. In **Chapter 3** I present results from an experiment which was conducted to study the impacts of different rice straw management methods typically performed by farmers of paddy fields. I expected that invertebrate decomposers might be more abundant and active in fields with rice straw amendment due to the higher structural diversity and food availability compared to fields where ash of burned straw was applied.

Implementing dry crops (like maize) in the crop cycle is an increasing trend that would reduce greenhouse gas emissions and water consumption. In the experiment presented in **Chapter 4** I tested how the soil fauna reacts to corresponding changes in the crop cycle and associated sudden changes in soil water availability between dry and wet seasons and what consequences arise for the rates of litter decomposition.

In **Chapter 5** I analyzed how the wide-spread invasive pest species *Pomacea canaliculata* L. (Golden Apple Snail) might contribute to the decomposition of rice straw. After a few weeks rice plants in the fields get unpalatable for the snails forcing them to switch to other food sources. I hypothesized that rice straw residuals are among the alternative forages and that the snails can therefore contribute to decomposition and nutrient supply in rice fields. We set up a laboratory experiment in which we analyzed their feeding activity and contribution to mass loss of rice straw as the only food resource.

REFERENCES OF CHAPTER 1

Anderson, J. M. 1988. Spatiotemporal effects of invertebrates on soil processes. Biology and fertility of soils **6**:216-227.

Bambaradeniya, C. N. B. 2000. Ecology and Biodiversity in an Irrigated Rice Field Ecosystem. University of Peradeniya, Sri Lanka.

Bambaradeniya, C. N. B., and F. P. Amarasinghe. 2003. Biodiversity associated with the rice field agroecosystem in Asian countries: A brief review. Working Paper 63, Colombo, Sri Lanka: International Water Management Institute.

Bardgett, R. D. 2005. The Biology of Soil - A community and ecosystem approach. Oxford University Press, Oxford.

Beare, M. H., M. V. Reddy, G. Tian, and S. C. Srivastava. 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of decomposer biota. Applied Soil Ecology **6**:87-108.

Berg, B., and C. McClaugherty. 2008. Plant litter - Decomposition, humus formation, carbon sequestration. second edition edition. Springer-Verlag Berlin Heidelberg.

Bhattacharyya, B., A. Basit, and D. K. Saikia. 2006. Parasitoids and predators of rice insect pests of Jorhat districts of Assam. Journal of Biological Control **20**:37.

Bhogal, A., S. D. Young, and R. Sylvester-Bradley. 1997. Straw incorporation and immobilization of spring-applied nitrogen. Soil Use and Management **13**:111-116.

Bollen, W. B. 1953. Mulches and soil conditioners: carbon and nitrogen in farm and forest products. Agric. Food Chain. **1**:379-381.

Bottrell, D. G., and K. G. Schoenly. 2012. Resurrecting the ghost of green revolutions past: The brown planthopper as a recurring threat to high-yielding rice production in tropical Asia. Journal of Asia-Pacific Entomology **15**:122-140.

Bray, F. 1979. Green Revolution: A New Perspective Green Revolution? Technology and Change in Rice-growing Areas of Tamil Nadu and Sri Lanka. Edited by B. H. Farmer. Cambridge Commonwealth series, Macmillan: London, 1977. Pp. xvi, 429. £12.00. Agriculture in the Peasant Sector of Sri Lanka. Edited by S. W. R. de A. Samarasinghe. Ceylon Studies Seminar, Peradeniya, Sri Lanka University Press: Colombo, 1977. Pp. xiv, 202. n.p. Agricultural Colonization in India Since Independence. By B. H. Farmer. Royal Institute of International Affairs, Oxford University Press: London, New York and Delhi, 1974. pp. xi, 372. £7.50. Modern Asian Studies **13**:681-688.

Bray, F. 1994. The Rice Economies - Technology & Development in Asian Societies. Reprint edition. University of California Press, Berkerley, United States.

Cancela da Fonseca, J. P., and S. Sarkar. 1998. Soil microarthropods in two different managed ecological systems (Tripura, India). Applied Soil Ecology **9**:105-107.

Canhoto, C., and M. A. S. Graça. 1995. Food value of introduced eucalypt leaves for a Mediterranean stream detritivore: Tipula lateralis. Freshwater Biology **34**:209-214.

Chaudhury, J., U. K. Mandal, K. L. Sharma, H. Ghosh, and B. Mandal. 2005. Assessing Soil Quality Under Long-Term Rice-Based Cropping System. Communications in Soil Science and Plant Analysis **36**:1141-1161.

Cheng, C. H. 1971. Effect of nitrogen application on the susceptibility of rice to brown planthopper attack. Journal of Taiwan Agricultural Research **20**:21-30.

Cohen, J. E., K. Schoenly, K. L. Heong, H. Justo, G. Arida, A. T. Barrion, and J. A. Litsinger. 1994. A Food Web Approach to Evaluating the Effect of Insecticide Spraying on

Insect Pest Population Dynamics in a Philippine Irrigated Rice Ecosystem. Journal of Applied Ecology **31**:747-763.

Cowie, R. H. 2002. Apple Snails (Ampullariidae) as Agricultural Pests: their Biology, Impacts and Management. Pages 145-193 *in* G. M. Barker, editor. Molluscs as crop pests. CAB International, Wallingford.

Drechsler, M., and J. Settele. 2001. Predator-prey interactions in rice ecosystems: effects of guild composition, trophic relationships, and land use changes - a model study exemplified for Philippine rice terraces. Ecological Modelling **137**:135-159.

Estebenet, A. L. 1995. Food and feeding in *Pomacea canaliculata* (Gastropoda: Ampullariidae). The Veliger **38**:277-283.

FAO. 2007. Food and Agriculture Organization of the United Nations. www.fao.org.

Fernando, C. H. 1977. Investigations on the aquatic fauna of tropical ricefields with special reference to South East Asia. Geo-Eco-Trop **3**:169-188.

Fernando, C. H. 1979. Ricefield ecosystems: a synthesis. Pages 939-942 *in* Tropical Ecology and Development: Proceedings of the 5th Int. Symp. of Tropical Ecology. International Society of Tropical Ecology, Kuala Lumpur.

Fernando, C. H. 1993. Rice field ecology and fish culture - an overview. Hydrobiologia **259**:91-113.

Ferreira, V., A. C. Encalada, and M. A. S. Graça. 2012. Effects of litter diversity on decomposition and biological colonization of submerged litter in temperate and tropical streams. Freshwater Science **31**:945-962.

Friebe, B., and W. Henke. 1991. Soil fauna and their straw decomposition capacity on reduced tillage. Z Kulturtech Landentw **32**:121-126.

García-Palacios, P., F. T. Maestre, J. Kattge, and D. H. Wall. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecology Letters **16**:1045-1053.

Gartner, T. B., and Z. G. Cardon. 2004. Decomposition dynamics in mixed-species leaf litter. Oikos **104**:230-246.

Gaud, W. S. 1968. The Green Revolution: Accomplishments and Apprehensions. Administrator, Agency for International Development, Department of State, AgBioWorld.

Gruner, H. E. 1993. Lehrbuch der speziellen Zoologie- Band 1: Wirbellose Tiere, 4. Teil: Arthropoda (ohne Insecta). Gustav Fischer Verlag, Jena, Stuttgart, New York.

Gurr, G. M., J. Liu, D. M. Read, J. L. A. Catindig, J. A. Cheng, L. P. Lan, and K. L. Heong. 2011. Parasitoids of Asian rice planthopper (Hemiptera: Delphacidae) pests and prospects for enhancing biological control by ecological engineering. Annals of applied biology **158**:149-176.

Gurr, G. M., D. M. Read, J. L. A. Catindig, J. Cheng, J. Liu, L. P. Lan, and K. L. Heong. 2012. Parasitoids of the rice leaffolder Cnaphalocrocis medinalis and prospects for enhancing biological control with nectar plants. Agricultural and Forest Entomology **14**:1-12.

Heal, O. W., J. M. Anderson, and M. J. Swift. 1997. Plant residue quality and decomposition: An historical overview. Pages 3-30 *in* G. Cadisch and K. E. Giller, editors. Driven by nature: plant Residue Quality and Decomposition. CAB International, Cambridge.

Heath, G. W., C. A. Edwards, and M. K. Arnold. 1964. Some methods for assessing the activity of soil animals in the breakdown of leaves. Pedobiologia **4**:80-87.

Heong, K. L., G. B. Aquino, and A. T. Barrion. 1991. Arthropod community structures of rice ecosystems in the Philippines. Bulletin of Entomological Research **81**:407-416.

Horgan, F. G., and E. Crisol. 2013. Hybrid rice and insect herbivores in Asia. Entomologia Experimentalis et Applicata **148**:1-19.

Houghton, R. A. 1995. Changes in the storage of terrestrial carbon since 1850. Pages 45-66 *in* R. Lal, J. Kimball, E. Levine, and B. A. Stewart, editors. Soils and global change. CRC Press, Boca Raton, Florida.

Ives, A. R., and W. H. Settle. 1997. Metapopulation dynamics and pest control in agricultural systems. American Naturalist **149**:220-246.

Jenkinson, D. S. 1977. Studies on the decomposition of plant material in soil. V. The effects of plant cover and soil type on the loss of carbon from14c labelled ryegrass decomposing under field conditions. Journal of Soil Science **28**:424-434.

Jiang, M. X., and J. A. Cheng. 2003. Interactions between the striped stem borer Chilo suppressalis (Walk.) (Lep., Pyralidae) larvae and rice plants in response to nitrogen fertilization. Anzeiger für Schädlingskunde = Journal of pest science **76**:124-128.

Kenmore, P. E., F. O. Cariño, C. A. Perez, V. A. Dyck, and A. P. Gutierrez. 1984. Population regulation of the rice brown planthopper (Nilaparvata lugens Stål) within rice fields in the Philippines. Journal of Plant Protection in the Tropics **1**:19-37.

Khandaker, A. H., T. Horiuchi, and S. Miyagawa. 2004. Effects of Powdered Rice Chaff on Growth and Yield of Rice Under Different Soil pH Conditions. Communications in Soil Science and Plant Analysis **35**:1469-1484.

Kiritani, K. 1992. Prospects for Integrated Pest Management. Japan Agricultural Research Quarterly **26**:81-87.

Klausnitzer, B. 2003. Insecta (Hexapoda), Insekten. Pages 601-681, 869-870 *in* W. Westheide and R. Rieger, editors. Spezielle Zoologie Teil 1: Einzeller und Wirbellose Tiere. Korrigierter und ergänzter Nachdruck. Spektrum Akademischer Verlag, Stuttgart, Heidelberg, Berlin.

Klotzbücher, T., A. Marxen, D. Vetterlein, J. Schneiker, M. Türke, N. van Sinh, N. H. Manh, H. van Chien, L. Marquez, S. Villareal, J. V. Bustamante, and R. Jahn. 2015. Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. Basic and Applied Ecology.

Knipling, E. F. 1972. Entomology and the Management of Man's Environment. Australian Journal of Entomology **11**:153-167.

Koegel-Knabner, I., W. Amelung, Z. Cao, S. Fiedler, P. Frenzel, R. Jahn, K. Kalbitz, A. Kölbl, and M. Schloter. 2010. Biogeochemistry of paddy soils. Geoderma **157**:1-14.

Kowalenko, C. G., K. C. Ivarson, and D. R. Cameron. 1978. Effects of moisture content, temperature and nitrogen fertilization on carbon dioxide evolution from field soils. Soil Biology & Biochemistry **10**:417-423.

Kumar, N., and R. Prasad. 2004. Effect of levels and sources of nitrogen on concentration and uptake of nitrogen by a high yielding variety and a hybrid of rice. Archives of Agronomy and Soil Science **50**:447-454.

Kurihara, Y. 1989. Ecology of Some Ricefields in Japan as Exemplified by Some Benthic Fauna, with Notes on Management. Internationale Revue der Gesamten Hydrobiologie **74**:507-548.

Lavelle, P., M. Dangerfield, C. Fragoso, V. Eschenbrenner, D. Lopez-Hernandez, B. Pashanasi, and L. Brussaard. 1994. The relationship between soil macrofauna and tropical soil fertility. Pages 137-169 *in* P. L. Woomer and M. J. Swift, editors. The Biological Management of Tropical Soil Fertility. Wiley, Chichester, UK.

Lekha, A., G. Chopra, and S. R. Gupta. 1989. Role of soil fauna in decomposition of rice and sorghum straw. Proceedings of the Indian Academy of Sciences **98**:275-284.

Liang, W., Q. Li, Y. Jiang, and D. A. Neher. 2005. Nematode faunal analysis in an aquic brown soil fertilised with slow-release urea, Northeast China. Applied Soil Ecology **29**:185-192.

Litsinger, J. A., and D. B. Estano. 1993. Management of the golden apple snail *Pomacea canaliculata* (Lamarck) in rice. Crop Protection **12**:363-370.

Lu, Z.-X., K.-L. Heong, X.-P. Yu, and C. Hu. 2004. Effects of Plant Nitrogen on Ecological Fitness of the Brown Planthopper, Nilaparvata lugens Stal. in Rice. Journal of Asia-Pacific Entomology **7**:97-104.

Mary, B., S. Recous, D. Darwis, and D. Robin. 1996. Interactions between decomposition of plant residues and nitrogen cycling in soil. Plant and Soil **181**:71-82.

Merckx, R., A. den Hartog, and J. A. van Veen. 1985. Turnover of root-derived material and related microbial biomass formation in soils of different texture. Soil Biology and Biochemistry **17**:565-569.

Nwilene, F. E., S. O. Oikeh, T. A. Agunbiade, O. Oladimeji, O. Ajayi, M. Sié, G. B. Gregorio, A. Togola, and A. D. Touré. 2008. Growing lowland rice: a production handbook. Africa Rice Center (WARDA).

Powell, J. R., D. Craven, and N. Eisenhauer. 2014. Recent trends and future strategies in soil ecological research—Integrative approaches at Pedobiologia. Pedobiologia **57**:1-3.

Rattanapun, W. 2012. Diversity and population dynamics of pests and predators in irrigated rice fields with treated and untreated pesticide. Communications in agricultural and applied biological sciences **77**:601-609.

Reddy, M. V., V. R. Reddy, D. F. Yule, A. L. Cogle, and P. J. George. 1994. Decomposition of straw in relation to tillage, moisture, and arthropod abundance in a semi-arid tropical Alfisol. Biology and fertility of soils **17**:45-50.

Reicosky, D. C., J. L. Hatfield, and R. L. Sass. 2000. Agricultural contributions to greenhouse gas emissions. Pages 37-55 *in* M. V. Reddy and H. F. Hodges, editors. Climate Change and Global Crop Productivity. CABI Publishing, Wallingford, UK.

Reissig, W. H. 1985. Illustrated guide to integrated pest management in rice in tropical Asia. International Rice Research Institute, Los Baños, Philippines.

Riutta, T., E. M. Slade, D. P. Bebber, M. E. Taylor, Y. Malhi, P. Riordan, D. W. Macdonald, and M. D. Morecroft. 2012. Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. Soil Biology and Biochemistry **49**:124-131.

Santos, P. F., and W. G. Whitford. 1981. The Effects of Microarthropods on Litter Decomposition in a Chihuahuan Desert Ecosystem. Ecology **62**:654-663.

Schmidt, A., H. Auge, R. Brandl, K. L. Heong, S. Hotes, J. Settele, S. Villareal, and M. Schädler. 2015a. Small-scale variability in the contribution of invertebrates to litter decomposition in tropical rice fields. DOI: 10.1016/j.baae.2015.01.006. Basic and Applied Ecology.

Schmidt, A., K. John, G. Arida, H. Auge, R. Brandl, F. G. Horgan, S. Hotes, L. Marques, N. Radermacher, J. Settele, V. Wolters, and M. Schädler. 2015b. Effects of residue management on decomposition in irrigated rice fields are not related to changes in the decomposer community. DOI: journal.pone.0134402. PLOS ONE.

Schoenly, K., J. E. Cohen, K. L. Heong, J. A. Litsinger, G. B. Aquino, A. T. Barrion, and G. Arida. 1996. Food web dynamics of irrigated rice fields at five elevations in Luzon, Philippines. Bulletin of Entomological Research **86**:451-466.

Settele, J. 1992. Auswirkungen der Intensivierung des Naßreisanbaus auf die terrestrischen Arthropodengemeinschaften philippinischer Reisterrassen. Margraf, Weikersheim, Germany.

Settele, J., I. Kühn, S. Klotz, G. Arida, E. Bergmeier, B. Burkhard, and e. al. 2015. A cultural landscapes and ecosystems services in south-east Asia – The LEGATO-project. Basic and Applied Ecology.

Settle, W. H., H. Ariawan, E. T. Astuti, W. Cahyana, A. L. Hakim, D. Hindayana, A. S. Lestari, and Pajarningsih. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology **77(7)**:1975-1988.

Simpson, I. C., P. A. Roger, R. Oficial, and I. F. Grant. 1993a. Density and composition of aquatic oligochaete populations in different farmers' ricefields. Biology and fertility of soils **16**:34-40.

Simpson, I. C., P. A. Roger, R. Oficial, and I. F. Grant. 1993b. Impacts of agricultural practices on aquatic oligochaete populations in ricefields. Biology and fertility of soils **16**:27-33.

Singh, Y., B. Singh, J. K. Ladha, C. S. Khind, T. S. Khera, and C. S. Bueno. 2004. Effects of Residue Decomposition on Productivity and Soil Fertility in Rice–Wheat Rotation. Soil Science Society of America Journal **68**:854-864.

Singh, Y., B. Singh, and J. Timsina. 2005. Crop residue management for nutrient cycling and improving soil productivity in rice-based cropping systems in the tropics. Advances in Agronomy **85**:269-407.

Storch, V., and U. Welsch. 1991. Systematische Zoologie - 4. Auflage. Gustav Fischer Verlag, Stuttgart, New York.

Swan, C. M., and M. A. Palmer. 2006. Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. Oecologia **147**:469-478.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkley and Los Angeles.

Thresh, J. M. 1989. Insect-borne viruses of rice and the green-revolution. Tropical Pest Management **35**:264-272.

Tian, G., L. Brussaard, and B. T. Kang. 1993. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions: effects on soil fauna. Soil Biology & Biochemistry **25**:731-737.

Tian, G., L. Brussaard, and B. T. Kang. 1995. An index for assessing the quality of plant residues and evaluating their effects on soil and crop in the (sub-)humid tropics. Applied Soil Ecology **2**:25-32.

Tian, G., B. T. Kang, and L. Brussaard. 1992. Effects of chemical composition on N, Ca, and Mg release during incubation of leaves from selected agroforestry and fallow plant species. Biogeochemistry **16**:103-119.

USDA. 2007. US Department of Agriculture. www.usda.gov.

Van Pham, C., S. Murayama, and Y. Kawamitsu. 2003. Heterosis for Photosynthesis, Dry Matter Production and Grain Yield in F1 Hybrid Rice (Oryza sativa L.) from Thermo-Sensitive Genic Male Sterile Line Cultivated at Different Soil Nitrogen Levels. Environment Control in Biology **41**:335-345.

Villegas-Pangga, G., G. Blair, and R. Lefroy. 2000. Measurement of decomposition and associated nutrient release from straw (Oryza sativa L.) of different rice varieties using a perfusion system. Plant and Soil **223**:1-11.

Visarto, P., M. P. Zalucki, H. J. Nesbitt, and G. C. Jahn. 2001. Effect of Fertilizer, Pesticide Treatment, and Plant Variety on the Realized Fecundity and Survival Rates of Brown Planthopper, Nilaparvata lugens (Stål) (Homoptera: Delphacidae) — Generating Outbreaks in Cambodia. Journal of Asia-Pacific Entomology **4**:75-84.

Wardle, D. A. 2002. Communities and Ecosystems: Linking the aboveground and belowground components. Princeton University Press, Princeton and Oxford.

Wassmann, R., R. S. Lantin, H. U. Neue, L. V. Buendia, T. M. Corton, and Y. Lu. 2000a. Characterization of Methane Emissions from Rice Fields in Asia. III. Mitigation Options and Future Research Needs. Nutrient Cycling in Agroecosystems **58**:23-36.

Wassmann, R., H. U. Neue, R. S. Lantin, K. Makarim, N. Chareonsilp, L. V. Buendia, and H. Rennenberg. 2000b. Characterization of Methane Emissions from Rice Fields in Asia. II. Differences among Irrigated, Rainfed, and Deepwater Rice. Nutrient Cycling in Agroecosystems **58**:13-22.

Weerakoon, A. C. J., and E. L. Samarasinghe. 1957. Mesofauna of the soil of a paddy-field in Ceylon - a preliminary survey. Ceylon Journal of Science (Biological Science) **1**:155-170.

Widyastuti, R. 2002. Soil fauna in rainfed paddy field ecosystems: their role in organic matter decomposition and nitrogen mineralization. Ecology and Development Series Band 3. Cuvillier Verlag, Göttingen.

Witkamp, M., and B. S. Ausmus. 1976. Processes in decomposition and nutrient transfer in forest ecosystems. Pages 375-396 *in* J. M. Anderson and A. Macfadyen, editors. The Role of Terrestrial and Aquatic Organisms in Decomposition Processes. Blackwell Scientific, Oxford.

Wolters, V. 1991. Soil Invertebrates - Effects on Nutrient Turnover and Soil Structure - A Review. Zeitschrift für Pflanzenernährung und Bodenkunde **154**:389-402.

Chapter 2

Small-scale Variability in the Contribution of Invertebrates to Litter Decomposition in Tropical Rice Fields

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ABSTRACT

Sustainable management of agricultural systems includes promoting nutrient cycles, which can reduce the need for application of fertilizer. As rice is one of the most important food resources in the world, sustainable management of rice paddies is increasingly in demand. However, little is known about the influence of invertebrates on decomposition processes in these ecosystems. We hypothesized that invertebrates contribute significantly to the decomposition of rice straw in paddies and that their relative contribution is affected by the distance to other landscape structures within fields. We placed rice straw in litterbags of two different mesh sizes which prevent (20 µm × 20 µm) or allow (5 mm × 5 mm) access of invertebrates in six irrigated rice fields for 84 days. In each field, bags were set on three transects running from the bund to the center of the field. Invertebrates significantly increased total rice straw litter mass loss by up to 45% (total decomposition: fine-meshed bags 64%; coarse-meshed bags 83%). Litter mass loss in bags accessed by invertebrates decreased with increasing distance from the bund. Such a spatial trend in litter mass loss was not observed in bags accessed only by microbes. Our results indicated that invertebrates can contribute to soil fertility in irrigated rice fields by decomposing rice straw, and that the efficiency of decomposition may be promoted by landscape structures around rice fields.

Keywords: Litter mass loss, detritivores, nutrient supply, *Oryza sativa*, litterbags, Philippines

ZUSAMMENFASSUNG

Nachhaltigkeit im bewässerten Tiefland-Reisanbau ist ein wesentlicher Bestandteil zur Sicherung der Nahrungsgrundversorgung eines großen Teils der Weltbevölkerung. Das Verständnis der komplexen Prozesse im Nährstoffkreislauf in Agrarökosystemen kann zu einer Erhöhung der Bodenfruchtbarkeit führen und den Bedarf an Düngemitteln drastisch reduzieren. Die Grundlage für eine natürliche Stickstoffzufuhr, zur Förderung des Pflanzenwachstums, ist die Zersetzung von totem organischem Material, was eine stabile Gemeinschaft von Bodenorganismen voraussetzt. Nichtsdestotrotz ist das Wissen über den Einfluss der Makrofauna auf Zersetzungsprozesse im Boden von Reisökosystemen rar.

Ziel dieser Studie war es, den Einfluss von Invertebraten auf die Zersetzungsrate von Reisstroh zu untersuchen und deren Effektivität in Abhängigkeit landschaftlicher Strukturvielfalt in direkter räumlicher Nähe zu den Untersuchungsflächen einzuschätzen. Um zu differenzieren, wie stark der jeweilige Anteil von Invertebraten und Mikroorganismen am Streuabbau ist, wurden Streubeutel mit zwei verschiedenen Maschenweiten (20 μm und 5 mm) verwendet und für 84 Tage auf die Bodenoberfläche bewässerter Reisfelder gelegt. Der Einfluss der Entfernung vom Reisfeldufer auf die Zersetzungsrate sollte mit Hilfe von Transekten, die vom Rand bis zur Mitte von sechs Versuchsfeldern gezogen wurden, ermittelt werden.

Invertebraten erhöhten nicht nur die Menge an insgesamt abgebautem Stroh bis zu 45%, verglichen mit der reinen mikrobiellen Zersetzung, ihr Einfluss nahm auch vom Rand zur Mitte des Feldes hin ab. Die Abbaurate der Mikroorganismen blieb innerhalb des Feldes dagegen relativ konstant.

Unsere Ergebnisse zeigen deutlich, dass Invertebraten einen großen Einfluss auf die Zersetzung von Reisstroh haben und damit die Bodenfruchtbarkeit positiv beeinflussen können. Zusätzlich konnte eine positive Korrelation zwischen Ufernähe und Abbaugeschwindigkeit von Invertebraten in Reisfeldern nachgewiesen werden, was auf eine höhere Nährstofffreisetzung in den Randbereichen der Felder hindeutet.

INTRODUCTION

The breakdown of organic matter is a crucial mechanism for nutrient cycling and productivity in terrestrial and aquatic ecosystems (Cebrian & Lartigue, 2004). Invertebrates play a key role in the decomposition process in both terrestrial (Swift, Heal, & Anderson, 1979) and aquatic systems (Webster & Benfield, 1986). Among other things, invertebrates break down bigger particles and make them available for microorganisms that decompose the material further and are responsible for nutrient release. These microorganisms are in turn one of the most important sources of energy for many soil (Swift et al., 1979) and aquatic animals (Hamilton, Lewis, & Sippel, 1992; Perry & Sheldon, 1986). Invertebrate decomposers are also known to act as scavengers (Parmenter & MacMahon, 2009). Besides their importance in the decomposition process, invertebrate decomposers were found to be an important food resource for predators (Ishijima et al., 2006; Oelbermann, Langel, & Scheu, 2008). In rice fields, for example, the use of decomposers, like chironomid larvae, as secondary food source allows generalist predators, as e.g. some groups of aquatic Heteroptera, to maintain high abundances throughout the whole rice cycle (Settle et al. 1996). Therefore, the role of invertebrate decomposers in food webs is crucial for the maintenance of ecosystem functions related to nutrient cycling, habitat structure, and community dynamics.

Rice cultivation is one of the most important, stable, and successful agricultural branches in tropical regions, especially in Southeast Asia (Kurihara, 1989). Toward the end of the Green Revolution, after the mid-1960s, rice production was intensified all over the world, especially in Asia (Bambaradeniya & Amarasinghe, 2003). The negative impacts of these agricultural practices for invertebrate food-webs in rice fields have been shown mainly for predators and parasitoids, which are the most important natural pest control agents (Drechsler & Settele, 2001; Ives & Settle, 1997; Schoenly et al., 1996), or on the pest species themselves (Cohen et al., 1994; Kiritani, 1992; Settele, 1992). In contrast, studies on the detritivorous invertebrate fauna in rice ecosystems focused solely on the diversity or the abundance of invertebrate decomposers (Simpson et al., 1993a, 1993b; Simpson et al., 1994) with only speculations about their functional role for decomposition and therefore nutrient dynamics. The lack of such studies in rice fields is surprising since the soil fauna is known to contribute substantially to nutrient dynamics and productivity in agro-ecosystems (Benckiser, 1997). Generally, there is no conceptual consensus about the role of invertebrate decomposers in freshwater ecosystems. Moreover, studies in tropical freshwater ecosystems have been done mainly in streams (Hagen et al., 2012), and to our knowledge, virtually no information on the contribution of invertebrates to litter decay in other tropical freshwater ecosystems, such as rice fields, is available. In general, the contribution of fauna to the decomposition process in the tropics is suggested to be high both in terrestrial and aquatic habitats (Wall et al. 2008). However, compared to terrestrial habitats invertebrate activity and litter characteristics might be of lower importance during the initial phase of litter decay in aquatic ecosystems as due to higher leaching of organic and mineral compounds mass loss tends to be high (Treplin & Zimmer, 2012).

The decomposition process in irrigated rice fields may differ from “real” aquatic systems in many aspects. For example, tillage and application of fertilizer and pesticides can change soil and water properties. Various studies have demonstrated an influence of nutrient concentrations in water on microbial-driven decomposition dynamics, with prevalent positive effects of nutrient addition on the decay rate (Webster & Benfield, 1986). Thus, the intensive application of fertilizers may lessen the relative importance of invertebrates in the decomposition process. Furthermore, fields are often irrigated only during certain periods of the year and regularly fall dry. Thus, macro-decomposers strictly bound to a water habitat may not establish stable populations or may not reach high abundances.

However, most aquatic invertebrate decomposers are not restricted to aquatic habitats throughout their life cycles. Some insects, which can be also found in irrigated rice fields, are involved in the decomposition process during their aquatic larval stages, e.g., chironomid larvae, and populate the surrounding terrestrial habitats as adults. The impact of surrounding landscape structures on ecosystem functions has repeatedly been shown for different arable fields (e.g., Perfecto, 2002; Diekötter et al., 2010; Woodcock et al., 2010). The spatial variability is often reflected by a decrease in diversity and corresponding ecosystem functions (e.g., pollination) in agro-ecosystems with increasing distance from surrounding landscape structures (e.g., Klein et al., 2003; Klein, 2009). However, invertebrate decomposers are often ignored in such studies despite their known importance for ecosystem functioning.

Here, we investigated whether invertebrate decomposers play an important role in the decomposition process and if this function is mediated by the distance from surrounding terrestrial habitats. As a proxy for decomposition we measured litter mass loss of rice straw in litterbags with and without access for invertebrates in paddy fields surrounded by six different landscape structures reflecting a broad spectrum of prevalent structures in the region of Laguna, Philippines. We tested the following hypotheses: (1) the invertebrate fauna contributes considerably to the litter mass loss of rice straw in paddy fields, and (2) the contribution of invertebrates to the decomposition process in rice fields decreases with increasing distance to the surrounding landscape structures. We assumed invertebrates to have a lower influence on litter mass loss in the middle of the fields, e.g., as many of them depend on surrounding structures in their adult stage (e.g. chironomids).

MATERIALS AND METHODS

Study site

The study was conducted in the Laguna province on the island of Luzon, Philippines, in one of the lowland, rice-dominated regions (Legato-site-label: PH_1; Klotzbücher et al., 2015) as part of the LEGATO project (Settele et al., 2015). Laguna lies southeast of the capital Manila (WGS84: 14.2 N; 121.4 E) and is characterized by a diverse landscape structure consisting of intensively used agricultural areas and near-natural forests, gardens, and various types of plantations. Field sites were located within an area of around 100 km^2. The soil in this area is of volcanic origin, and a high proportion consists of clay and loam. The aquatic decomposer mesofauna is dominated by annelids, nematodes and chironomid larvae with other invertebrate groups in smaller abundances (unpubl.).

Wet rice in the lowlands of Luzon Island (Philippines) is mostly cultivated in two crop cycles per year, one in the dry season (December–May) and one in the wet season (June–November). A crop cycle (without the fallow period) lasts around 100 days. Our study was carried out during the wet season from June to September in 2012. During this time, the monthly rainfall varied between 75 and 465 mm, and the average temperature varied between 25 and 25.9 °C. Weather data were provided by the Climate Unit of the International Rice Research Institute, Los Baños, Laguna, Philippines.

Around 20 days after seed sowing, rice seedlings were transplanted separately in the field. Paddies were drained 2–3 weeks before harvesting, i.e., 80–90 days after transplanting.

Study design

Six rice fields surrounded by different landscape elements, representative for the region, were chosen (Table 1). Field management was carried out according to the usual management scheme including fertilizers, pesticides etc. It is important to note that this study was not designed to compare different landscape structures, but to get an idea about how structures around rice fields in general can affect invertebrate contribution to litter mass loss.

To investigate the contribution of invertebrates to litter mass loss, we placed 10 g of litter (air-dried rice straw; *Oryza sativa*, variety NSIC Rc 222) in 15 cm × 20 cm nylon bags of two mesh sizes: fine, 20 μm × 20 μm mesh size, which gives access to microbes (bacteria, fungi, etc.) only; and coarse, 5 mm × 5 mm mesh size, which gives access also to invertebrates (Tian, Kang, & Brussaard, 1992). The filled litterbags were set in the fields in June/July 2012 after rice seedlings had been transplanted. Pairs of bags, one fine and one coarse meshed, were placed along three transect lines on the soil surface in every field and fixed to the ground by coarse nylon nets and bamboo sticks. Transect lines in each field were 4 m apart and reached from the bund to the middle of the field (7.5 ± 1.9 m mean ± SD). Due to the different dimensions of the fields transect lines varied in length. Depending on the size of the particular field, 5–10 pairs of bags were placed on each transect line, with 1 m between each pair; the first pair was placed directly next to the bund, but still within the field. The two bags of one pair were placed directly next to each other with no space in between. Litterbag gradients were always established from one particular border of the field and if a site neighbored the respective structure on one side only, this side was chosen.

Litterbags were retrieved 84 days after setting and before rice harvesting in August/September 2012. Soil particles, roots, and other alien plant material adhering to the litter were removed, and the remaining straw was dried at 60 °C for 3 days and weighed to the nearest centigram.

Data analysis

To account for the difference in weight between air-dried and oven-dried straw several samples of air-dried straw were weighed before and after drying in the oven for 3 days at 60 °C. The average weight loss of all samples due to moisture loss was then subtracted from the original 10 g before calculating litter mass losses. The percent loss in litter mass was logit transformed prior to all statistical analyses for approximation of normal distribution and reduction of variance heterogeneity. Using a nested general linear mixed model (GLMM) type III sum of squares (procedure MIXED, SAS 9.2.), litter mass loss was analyzed in dependence on *mesh size*, *site*, and the co-variable *distance from bund*. Transects were considered random and nested in *site*. The least-square means were calculated for the six levels of the factor *site*. To illustrate the contribution of invertebrate decomposers to litter mass loss depending on the distance to the bund within a paddy, the percentage litter mass loss was normalized to the specific effects of the factor *site*. This was done by subtracting the particular estimated mean value for each site from the corresponding logit-transformed litter mass loss.

RESULTS

At all six sites, the mean litter mass loss of the coarse-meshed bags (83 ± 8%, mean ± SD) was higher than in fine-meshed bags (64 ± 7.5%, mean ± SD) (Fig. 1). Thus, invertebrates had a significant influence on litter mass loss (highly significant factor *mesh size*; Table 2). However, litter mass loss due to invertebrates varied across sites (significant *mesh size* × *site* interaction; Table 2).

Across all sites, the overall litter mass loss in coarse-meshed bags decreased with increasing distance from the bund of the paddy (Fig. 2). The overall litter mass loss in fine-meshed bags, however, stayed relatively constant at the different locations within the field. These results indicated that the invertebrate contribution to litter mass loss decreased with increasing distance from the bund.

Furthermore, the effect of distance from the bund varied across sites (significant *site* × *distance from bund* interaction; Table 2). At four sites (landscape structures: vines, rice, bushes, and forest), litter mass loss decreased with increasing distance to the bund. At the other two sites (with structures farm and wild meadow) litter mass loss increased with increasing distance to the bund, but R^2 values indicated stronger negative correlations than positive ones (Fig. 3).

Table 1 Description of the six study sites and their different surrounding structures.

Site label	Area (m^2)	Description of adjacent surroundings
“Forest”	1,200	3 sides - forest; 1 side - rice
“Bushes”	2,000	2 sides - approx. 20 m wide strip of shrub land (bordering a forest); 2 sides - rice
“Rice”	800	4 sides - rice
“Wild meadow”	1,600	1 side - wild unmanaged area; 3 sides - rice
“Farm”	600	1 side - area with a house incl. a small yard with free-range chickens; 3 sides - rice
“Vine”	500	1 side - vines; 3 sides - rice

Table 2 Effects of *mesh size*, *site*, and *distance from bund* as well as their interactions on mass loss of rice straw litter (logit-transformed) using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Factors	Decomposition rate		
	df	F	*P*
Mesh size	1	180	< **0.001**
Site	5	7.83	**0.002**
Distance from bund	1	13.8	**0.003**
Mesh size × Site	5	5.13	**0.01**
Mesh size × Distance from bund	1	11.7	**0.01**
Distance from bund × Site	5	4.61	**0.01**
Distance from bund × Mesh size × Site	5	2.88	0.06

Factor *mesh size* represents the bags of two mesh sizes (5 mm × 5 mm and 20 µm × 20 µm) used in every plot, factor *site* represents the six fields with different surrounding landscape structures, and the co-variable *distance from bund* represents the continuous effect of the location of litterbags within the fields (linearly from the bund to the middle of the field). The model also includes the random effect *transect* nested in *site* (three transect lines per site); the factor itself and its interactions are not shown.

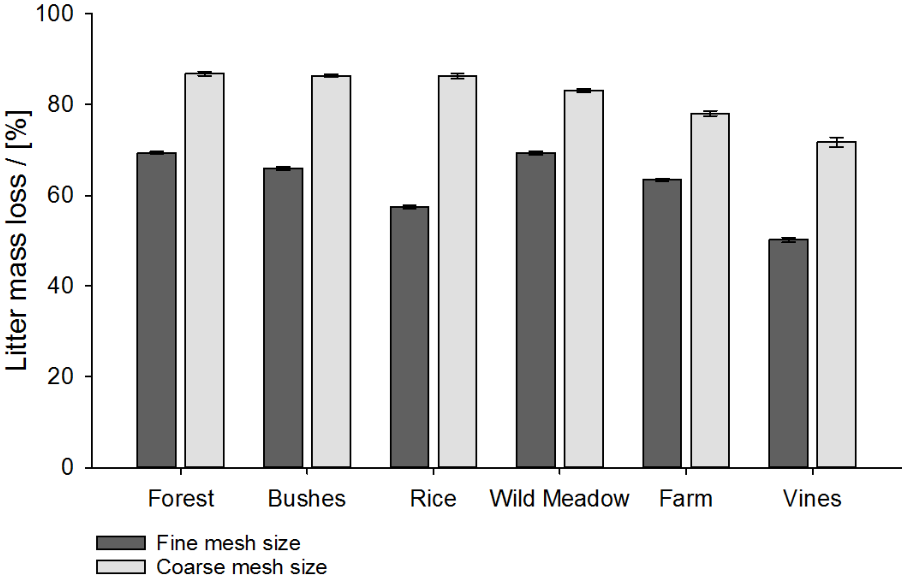

Figure 1 Percent litter mass loss in fine-meshed and coarse-meshed litterbags at the six sites with different surrounding landscape structures (means ± SE).

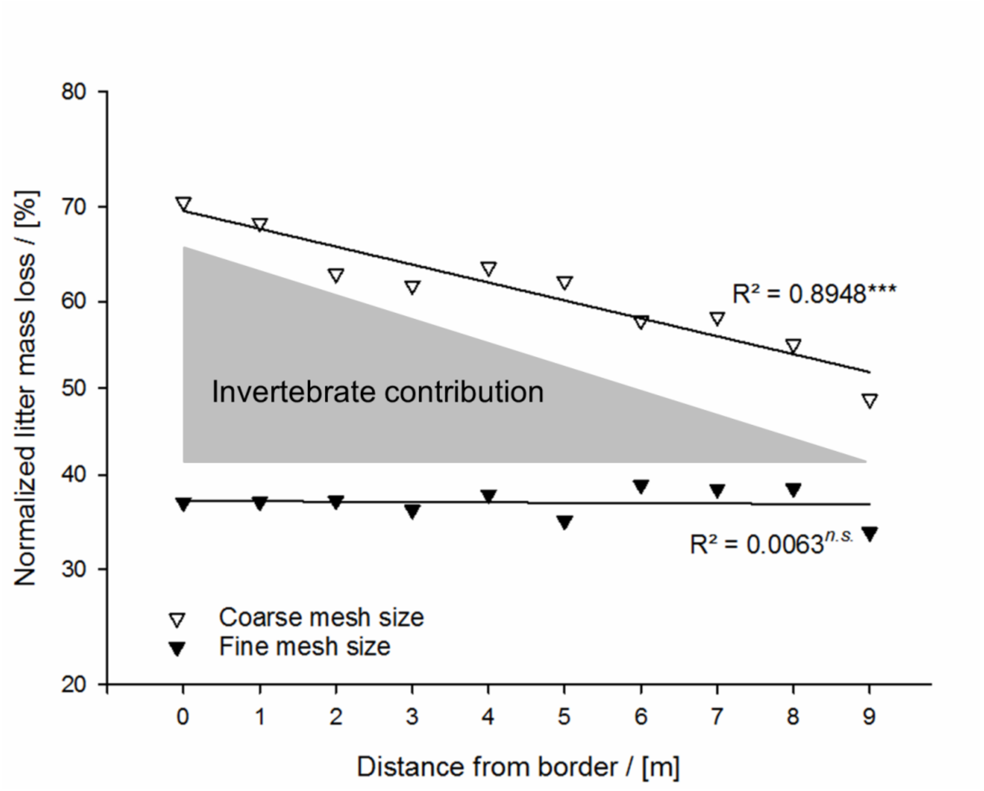

Figure 2 Correlation of percent litter mass loss from fine- and coarse-meshed bags with *distance from border*. R^2 values indicate the strength of the correlations ($p>0.05^{n.s.}$; $p\leq0.001^{***}$). Percentage litter mass loss was controlled for site effects.

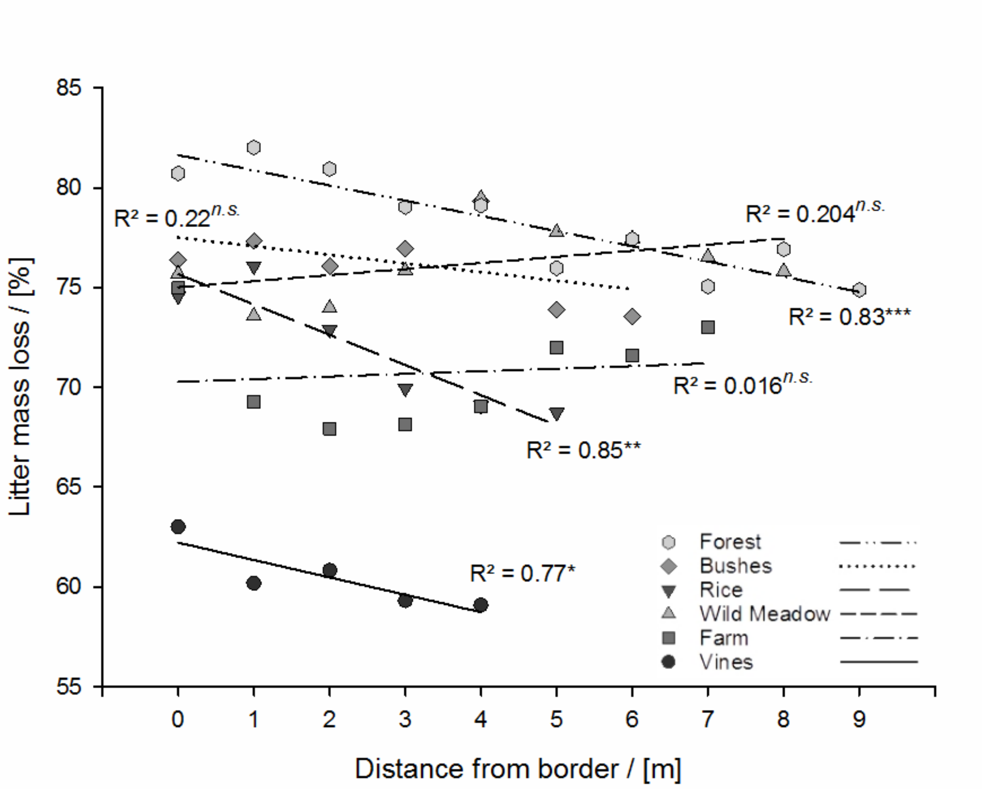

Figure 3 Correlation of mean percent litter mass loss at the six sites with *distance from border*. R^2 values indicate the strength of the correlations ($p>0.05^{n.s.}$; $p\leq0.05$*, $p\leq0.01$**, $p\leq0.001$***).

DISCUSSION

Although the potential of decomposition of straw from cereals for soil fertility and site productivity has been highlighted in several studies (Bhogal et al., 1997; Mary et al., 1996; Singh et al., 2004), the importance of invertebrate decomposers in rice paddies has been underestimated and rarely studied in the past (Settle et al., 1996). The results reported here support our hypothesis that invertebrates significantly contribute to litter mass loss of rice straw in tropical paddy fields. Hence, invertebrates might be crucial for the establishment of sustainable agriculture in rice-dominated areas by increasing the soil fertility in irrigated rice fields. As the field management was done as ‘business as usual’, pesticides might have had negative effects on the invertebrate abundance during our study. The effect of the invertebrate fauna on decomposition could therefore have been underestimated, making our results a conservative measure of their contribution and our conclusions on their potential role in ecosystem functioning even more robust. As our study was carried out in conventionally managed rice fields, our results reflect the processes invertebrates have on decomposition in a much more realistic way than a study on pesticide free paddies could have achieved.

Most invertebrate decomposers in freshwater systems are not restricted to aquatic habitats throughout their life cycles. Therefore, the abundance, diversity and species composition of invertebrates in rice fields might be closely linked to the surrounding landscape. Using litter mass loss as proxy we hypothesized that the contribution of invertebrates to the decomposition process in rice fields decreases with increasing distance to the bunds. Overall, we found that invertebrate decomposition indeed declined with increasing bund distance. One reason for this could be the heterogeneous within-field flooding where paddies are often more constantly flooded at the borders than in the middle, which would negatively affect aquatic invertebrates along with their decomposition activity. In contrast, litter mass loss of rice straw assigned to microbial decay activity was not affected by the distance to the bunds and microbial decay processes are also known to be sensitive to changes in water availability. For example, studies in peat soils showed that microorganisms are very sensitive to water and oxygen availability (Jaatinen et al., 2007; Kwon et al., 2013). A drop in water along with the consequential increased oxic conditions would result in a shift of the microbial community structure (Kwon et al., 2013) and an increase in microbial biomass (Mäkiranta et al., 2009) and activity (Freeman et al., 1996) and therefore lead to a drastic increase of the microbial decay rate. As this was not the case, the observed decrease of invertebrate decomposition activity with increasing distance to the surroundings can probably be attributed to the spatial effects of the surrounding landscapes themselves and not to a decrease in water availability in the middle of the field. Future studies should investigate if different landscape structures also have different effects on decomposer invertebrates, which would account for the importance of structural diversity also at smaller spatial scales and the necessity to conserve and establish a certain level of landscape heterogeneity for sustainable and ecological rice agriculture.

When we examined the spatial effects within the fields on the total litter mass loss assigned to invertebrate and microbial decomposition, differences between the six fields became apparent. In two of the six fields the litter mass loss increased with increasing distance from the bund. In contrast, the other four fields showed the reverse pattern, i.e., litter mass loss decreased with increasing distance from the bund. As our study was not intended to describe differences between specific landscape structures, our design only allows us to interpret the general patterns a set of landscape structures has on litter mass loss and how invertebrates are influenced by them. As we only sampled during one season and only during the irrigated phase of the rice paddy cycle, possible reasons for the contrasting patterns between sites could be different water depths, which can range between 5 and 30 cm, or varying durations of flooding (Bambaradeniya & Amarasinghe, 2003). More shallow water depths result in higher and more rapidly changing temperatures and oxygen levels, especially between day and night (Bambaradeniya & Amarasinghe, 2003). As stated above, invertebrates as well as microorganisms are quite sensitive to rapid environmental changes, which is why different patterns of litter mass losses assigned to their joint decomposition activities can arise between sites.

Our study aimed at demonstrating the general importance of invertebrate decomposers in rice fields. Future studies should extend the period of investigation up to at least two rice cycles and focus on a systematic comparison of how differently structured surroundings of paddy fields influence the activity of invertebrate decomposers. Especially the question whether intensively used and therefore more homogeneous landscapes support a lower diversity and abundance of decomposer invertebrates should receive attention. The results of such studies would help in establishing and maintaining diverse structures with sustainable ecosystem functions at local and regional scales.

CONCLUSION

In our study, we demonstrated that invertebrate decomposers substantially contribute to the decomposition process in irrigated rice fields. Our results indicated that invertebrate decomposers can be expected to be important for soil fertility and site productivity. Crop residue management strategies should consider invertebrates when using straw to improve soil conditions. The contribution of invertebrates to the litter mass loss of rice straw, as a proxy for decomposition, decreased with increasing distance to the bund on most sites tested, which could indicate that the surrounding landscape structure may influence the assemblages of invertebrate decomposers. Future studies should evaluate in more detail how land management and landscape structure surrounding rice fields contribute to the maintenance of ecosystem services, such as nutrient cycling provided by invertebrate decomposers.

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REFERENCES OF CHAPTER 2

Bambaradeniya, C. N. B., & Amarasinghe, F. P. (2003). *Biodiversity associated with the rice field agroecosystem in Asian countries: A brief review.* Working Paper 63. Colombo, Sri Lanka: International Water Management Institute.

Benckiser, G. (1997). *Fauna in soil ecosystems: recycling processes, nutrient fluxes, and agricultural production* (G. Benckiser Ed.). New York, USA: CRC Press.

Bhogal, A., Young, S. D., & Sylvester-Bradley, R. (1997). Straw incorporation and immobilization of spring-applied nitrogen. *Soil Use and Management, 13*, 111-116.

Cebrian, J., & Lartigue, J. (2004). Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecological Monographs, 74*(2), 237-259. doi: 10.1890/03-4019

Cohen, J. E., Schoenly, K., Heong, K. L., Justo, H., Arida, G., Barrion, A. T., et al. (1994). A Food Web Approach to Evaluating the Effect of Insecticide Spraying on Insect Pest Population Dynamics in a Philippine Irrigated Rice Ecosystem. *Journal of Applied Ecology, 31*(4), 747-763.

Diekötter, T., Wamser, S., Wolters, V., & Birkhofer, K. (2010). Landscape and management effects on structure and function of soil arthropod communities in winter wheat. *Agriculture, Ecosystems & Environment, 137*(1-2), 108-112. doi: 10.1016/j.agee.2010.01.008

Drechsler, M., & Settele, J. (2001). Predator-prey interactions in rice ecosystems: effects of guild composition, trophic relationships, and land use changes - a model study exemplified for Philippine rice terraces. *Ecological Modelling, 137*(2-3), 135-159.

Freeman, C., Liska, G., Ostle, N. J., Lock, M. A., Reynolds, B., & Hudson, J. (1996). Microbial activity and enzymic decomposition processes following peatland water table drawdown. *Plant and Soil, 180*(1), 121-127. doi: 10.1007/BF00015418

Hagen, E. M., McCluney, K. E., Wyant, K. A., Soykan, C. U., Keller, A. C., Luttermoser, K. C., et al. (2012). A meta-analysis of the effects of detritus on primary producers and consumers in marine, freshwater, and terrestrial ecosystems. *Oikos, 121*(10), 1507-1515. doi: 10.1111/j.1600-0706.2011.19666.x

Hamilton, S. K., Lewis, W. M., Jr., & Sippel, S. J. (1992). Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. *Oecologia, 89*(3), 324-330. doi: 10.1007/BF00317409

Ishijima, C., Taguchi, A., Takagi, M., Motobayashi, T., Nakai, M., & Kunimi, Y. (2006). Observational evidence that the diet of wolf spiders (Araneae: Lycosidae) in paddies temporarily depends on dipterous insects. *Applied Entomology and Zoology, 41*(2), 195-200. doi: 10.1303/aez.2006.195

Ives, A. R., & Settle, W. H. (1997). Metapopulation dynamics and pest control in agricultural systems. *American Naturalist, 149*(2), 220-246.

Jaatinen, K., Fritze, H., Laine, J., & Laiho, R. (2007). Effects of short- and long-term water-level drawdown on the populations and activity of aerobic decomposers in a boreal peatland. *Global Change Biology, 13*(2), 491-510. doi: 10.1111/j.1365-2486.2006.01312.x

Kiritani, K. (1992). Prospects for Integrated Pest Management. *Japan Agricultural Research Quarterly, 26*, 81-87.

Klein, A.-M. (2009). Nearby rainforest promotes coffee pollination by increasing spatio-temporal stability in bee species richness. *Forest Ecology and Management, 258*(9), 1838-1845. doi: 10.1016/j.foreco.2009.05.005

Klein, A. M., Steffan–Dewenter, I., & Tscharntke, T. (2003). Fruit set of highland coffee increases with the diversity of pollinating bees. *Royal Society Publishing, 270*(1518), 955-961. doi: 10.1098/rspb.2002.2306

Klotzbücher, T., Marxen, A., Vetterlein, D., Schneiker, J., Türke, M., van Sinh, N., et al. (2015). Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. *Basic and Applied Ecology*. doi: 10.1016/j.baae.2014.08.002

Kurihara, Y. (1989). Ecology of Some Ricefields in Japan as Exemplified by Some Benthic Fauna, with Notes on Management. *Internationale Revue der Gesamten Hydrobiologie, 74*(5), 507-548.

Kwon, M. J., Haraguchi, A., & Kang, H. (2013). Long-term water regime differentiates changes in decomposition and microbial properties in tropical peat soils exposed to the short-term drought. *Soil Biology and Biochemistry, 60*, 33-44. doi: 10.1016/j.soilbio.2013.01.023

Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J., & Minkkinen, K. (2009). Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. *Soil Biology and Biochemistry, 41*(4), 695-703. doi: 10.1016/j.soilbio.2009.01.004

Mary, B., Recous, S., Darwis, D., & Robin, D. (1996). Interactions between decomposition of plant residues and nitrogen cycling in soil. *Plant and Soil, 181*(1), 71-82. doi: 10.1007/BF00011294

Oelbermann, K., Langel, R., & Scheu, S. (2008). Utilization of prey from the decomposer system by generalist predators of grassland. *Oecologia, 155*(3), 605-617. doi: 10.1007/s00442-007-0927-4

Parmenter, R. R., & MacMahon, J. A. (2009). Carrion decomposition and nutrient cycling in a semiarid shrub–steppe ecosystem. *Ecological Monographs, 79*(4), 637-661. doi: 10.1890/08-0972.1

Perfecto, I., & Vandermeer, J. (2002). Quality of Agroecological Matrix in a Tropical Montane Landscape: Ants in Coffee Plantations in Southern Mexico Calidad de la Matriz Agroecológica en un Paisaje Montañoso Tropical: Hormigas en Plantaciones de Café en el Sur de México. *Conservation Biology, 16*(1), 174-182. doi: 10.1046/j.1523-1739.2002.99536.x

Perry, S. A., & Sheldon, A. L. (1986). Effects of exported seston on aquatic insect faunal similarity and species richness in lake outlet streams in Montana, USA. *Hydrobiologia, 137*(1), 65-77. doi: 10.1007/BF00004174

Schoenly, K., Cohen, J. E., Heong, K. L., Litsinger, J. A., Aquino, G. B., Barrion, A. T., et al. (1996). Food web dynamics of irrigated rice fields at five elevations in Luzon, Philippines. *Bulletin of Entomological Research, 86*, 451-466.

Settele, J. (1992). *Auswirkungen der Intensivierung des Naßreisanbaus auf die terrestrischen Arthropodengemeinschaften philippinischer Reisterrassen* (Vol. 10 (3)). Weikersheim, Germany: Margraf.

Settele, J., Kühn, I., Klotz, S., Arida, G., Bergmeier, E., & Burkhard, B., et al. (2015). A cultural landscapes and ecosystems services in south-east Asia – The LEGATO-project. *Basic and Applied Ecology*.

Settle, W. H., Ariawan, H., Astuti, E. T., Cahyana, W., Hakim, A. L., Hindayana, D., et al. (1996). Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology, 77(7)*, 1975-1988.

Simpson, I. C., Roger, P. A., Oficial, R., & Grant, I. F. (1993a). Density and composition of aquatic oligochaete populations in different farmers' ricefields. *Biology and fertility of soils, 16*(1), 34-40. doi: 10.1007/BF00336512

Simpson, I. C., Roger, P. A., Oficial, R., & Grant, I. F. (1993b). Impacts of agricultural practices on aquatic oligochaete populations in ricefields. *Biology and fertility of soils, 16*(1), 27-33. doi: 10.1007/BF00336511

Simpson, I. C., Roger, P. A., Oficial, R., & Grant, I. F. (1994). Effects of nitrogen fertilizer and pesticide management on floodwater ecology in a wetland ricefield. *Biology and fertility of soils, 17*(2), 138-146. doi: 10.1007/BF00337746

Singh, Y., Singh, B., Ladha, J. K., Khind, C. S., Khera, T. S., & Bueno, C. S. (2004). Effects of Residue Decomposition on Productivity and Soil Fertility in Rice–Wheat Rotation. *Soil Science Society of America Journal, 68*(3), 854-864. doi: 10.2136/sssaj2004.8540

Swift, M. J., Heal, O. W., & Anderson, J. M. (1979). *Decomposition in terrestrial ecosystems*. Berkley and Los Angeles: University of California Press.

Tian, G., Kang, B. T., & Brussaard, L. (1992). Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions - decomposition and nutrient release. *Soil Biology & Biochemistry, 24*(10), 1051-1060.

Treplin, M., & Zimmer, M. (2012). Drowned or Dry: A Cross-Habitat Comparison of Detrital Breakdown Processes. *Ecosystems, 15*(3), 477-491. doi: 10.1007/s10021-012-9523-5

Wall, D. H., Bradford, M. A., St. John, M. G., Trofymow, J. A., Behan-Pelletier, V., Bignell, D. E., et al. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*. doi: 10.1111/j.1365-2486.2008.01672.x

Webster, J. R., & Benfield, E. F. (1986). Vascular Plant Breakdown in Freshwater Ecosystems. *Annual Review of Ecology and Systematics, 17*(1), 567-594. doi: doi:10.1146/annurev.es.17.110186.003031

Woodcock, B. A., Redhead, J., Vanbergen, A. J., Hulmes, L., Hulmes, S., Peyton, J., et al. (2010). Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. *Agriculture, Ecosystems & Environment, 139*(1-2), 181-186. doi: 10.1016/j.agee.2010.07.018

Chapter 3

EFFECTS OF RESIDUE MANAGEMENT ON DECOMPOSITION IN IRRIGATED RICE FIELDS ARE NOT RELATED TO CHANGES IN THE DECOMPOSER COMMUNITY

Schmidt, A., K. John, G. Arida, H. Auge, R. Brandl, F. G. Horgan, S. Hotes, L. Marques, N. Radermacher, J. Settele, V. Wolters, and M. Schädler (2015). DOI: journal.pone.0134402. *PLOS ONE.*

ABSTRACT

Decomposers provide an essential ecosystem service that contributes to sustainable production in rice ecosystems by driving the release of nutrients from organic crop residues. During a single rice crop cycle we examined the effects of four different crop residue management practices (rice straw or ash of burned straw scattered on the soil surface or incorporated into the soil) on rice straw decomposition and on the abundance of aquatic and soil-dwelling invertebrates. Mass loss of rice straw in litterbags of two different mesh sizes that either prevented or allowed access of meso- and macro-invertebrates was used as a proxy for decomposition rates. Invertebrates significantly increased total loss of litter mass by up to 30 %. Initially, the contribution of invertebrates to decomposition was significantly smaller in plots with rice straw scattered on the soil surface; however, this effect disappeared later in the season. We found no significant responses in microbial decomposition rates to management practices. The abundance of aquatic fauna was higher in fields with rice straw amendment, whereas the abundance of soil fauna fluctuated considerably. There was a clear separation between the overall invertebrate community structure in response to the ash and straw treatments. However, we found no correlation between litter mass loss and abundances of various lineages of invertebrates. Our results indicate that invertebrates can contribute to soil fertility in irrigated paddy fields by decomposing rice straw, and that their abundance as well as efficiency in decomposition may be promoted by crop residue management practices.

Keywords: Litter mass loss, detritivores, litterbags, aquatic fauna, soil fauna, *Oryza sativa*, tropics, Southeast Asia, Philippines

INTRODUCTION

Establishing sustainable agricultural practices together with the restoration of functional food webs for integrated pest management and nutrient cycling has become a major focus of current rice research. Decomposition in general, and decomposition of rice straw in particular, is an important process regulating energy flows and nutrient cycles in rice paddies [1-3]. Therefore, the establishment of a functional decomposer community is essential in the development of practices for sustainable agricultural management in rice dominated landscapes [4]. However, to date, decomposition dynamics (e.g. interactions between microbes and invertebrates) as well as detritivore community assembly in flooded rice ecosystems have received little research attention. The present study examines the effects of different crop residue management practices on invertebrate communities and decomposition rate in tropical rice fields.

Rice straw decomposition by invertebrate decomposers is likely to be of particular importance to the stable and adequate availability of nutrients and to sustained soil quality in rice fields, because under the anaerobic conditions created by flooding microbial decomposition rates are expected to be low [5-10]. Therefore, major component of our study was to evaluate the contribution of invertebrates to litter decomposition in tropical irrigated rice fields. However, the complex relationship between soil biodiversity and ecosystem function is poorly understood [8, 11-14]. The effects of soil invertebrates on litter decomposition are often rather indirect; nevertheless, the activity of soil invertebrates is an essential determinant of decomposition rates and nutrient release [10, 15-17]. For example, litter fragmentation by invertebrates enhances microbial decomposition by increasing the surface area of plant fragments which creates a more stable and favorable micro-environment for decomposer microbes [1, 18].

The activity of invertebrate and microbial decomposers depends primarily on moisture and temperature [18-22], but also depends on the quality of the litter, e.g. lignin concentrations [23] and C/N ratios [3, 15]. Decomposers generally prefer high quality substrates with low C/N ratios, which results in faster decay rates [9, 24, 25]. Rice straw residues have high C/N ratios (approx. 61, see S1 Fig.) compared to litter from other herbaceous plants (e.g. ranging from 19 to 30; see [26]); nevertheless, rice straw represents an important carbon and nitrogen source in rice paddies [20, 27]. Crop residues are often burned by farmers for cost-effectiveness or for the lack of alternative technology to incorporate large amounts of residues into the soil [18, 28, 29]. This results in a loss of both C and N [20]. Recently, an awareness of the importance of rice straw for nutrient supply has led to increasing efforts to improve strategies of crop residue management [18, 30]. Several studies have indicated that rice straw increases the content of mineralized N in the soil [31-33] and can improve crop yields (e.g. [34]). Therefore, the incorporation of rice straw residues into the paddy soil can further reduce N losses and enhance N availability for plants [35].

Rice fields provide habitat for a bewildering variety of soil-dwelling and freshwater animals [36, 37]. The most abundant groups of invertebrates involved in decomposition in flooded rice fields are oligochaetes, like *Enchytraeidae* or *Tubificidae*, chironomid larvae, nematodes and microcrustaceans. As an essential driver regulating nutrient cycling processes [1, 38] these organisms may increase paddy soil fertility [39]. In contrast, soil-dwelling microarthropods, like *Acari* or *Collembola*, occur in comparatively low numbers and are therefore thought to have limited influence on decomposition processes in irrigated rice [38, 40, 41].

Under aquatic conditions, litter initially decomposes at a fast rate due to leaching of water soluble substances [1]. It has been repeatedly demonstrated for flooded rice fields that after this initial rapid phase with large reductions in litter biomass, decomposition rates eventually slow down as soluble components become exhausted [14]. Deceleration of decomposition in tropical aquatic systems may also be due to a gradual decrease in fungal biomass over time [9], which makes the litter less attractive for decomposer organisms, especially grazers.

The results of previous studies that examined the effects of crop residue management on faunal diversity and abundance have been generally inconsistent. There is general agreement that management practices in flooded paddy fields do not affect the species richness of the aquatic and soil fauna [42, 43], but do affect relative abundance and, therefore, the composition of these species assemblages. Friebe and Henke [44] indicated that greater tillage intensity was associated with significantly lower abundances of soil fauna, which also decreased rates of straw decomposition. In contrast, Singh et al. [18] presented evidence of a positive effect of the incorporation of crop residues into soil on populations of all groups of macro- and microorganisms. Therefore, in the present study, we examine how management practices influence the composition and abundance of different functional groups of aquatic and soil fauna and whether this fauna contributes to straw decomposition in tropical flooded rice fields. For this, we investigated common practices of residue management that differed in the materials applied (ash *vs*. straw) and the mode of application (scattering on the surface *vs*. incorporating in the soil).

We tested the following hypotheses:

(1) Invertebrates contribute significantly to the mass loss of rice straw in paddy fields, with (2) the abundances of invertebrates being higher in rice fields with straw amendment compared to ash treatment. (3) This effect depends on the mode of residue application since scattering residues on the surface might favor different groups of invertebrates (henceforth lineages) from those favored when the material is incorporated into the soil. (4) Abundances of functional groups of invertebrates and their relative contribution to decomposition will vary over time with stronger effects of invertebrates and faster decomposition rates at the beginning of the season.

MATERIAL AND METHODS

Study site

As part of the LEGATO project [45] our decomposition experiment was conducted at the field research station of the Philippine Rice Research Institute (PhilRice) in Muñoz, Nueva Ecija province on the island of Luzon, Philippines (elevation: 50 m above sea level; latitude 15.67, longitude 120.89 WGS84 decimal degrees; LEGATO region: PH_2, [46]). The soil in this area is of volcanic origin with a high proportion of clay and loam. In this region, lowland flooded rice is mostly cultivated in two crop cycles per year, one in the dry season (January - April) and one in the wet season (June - September). Our study was carried out during the dry season of 2013. During the experiments, the average temperature was between 25.8 °C and 29.6 °C, and the monthly rainfall varied between 0 and 2 mm (weather data provided by PhilRice - Central Experiment Station). The experimental site had previously been used for wet-rice cultivation for about 50 years. As the experiment was conducted at the field research station of the Institute, the rice fields of our study were not “true” farmers' fields, but were created just for this experiment. The experiment was carried out with the permission of and in cooperation with researchers of PhilRice. Our study did not involve any endangered or protected species.

Study design

The experiment was arranged as a randomized complete block design with five blocks, each with five plots, and arranged in a 5 × 5 grid (S2 Fig.). Each plot had a surface area of 25 m^2. Four crop residue management treatments were applied randomly to the plots within each of the five blocks four days prior to planting the rice seedlings. Treatments included: ash of burned rice straw scattered on the field (henceforth abbreviated by ‘Asc’), ash of burned rice straw mixed in the soil (‘Ami’), rice straw scattered on the field (‘Ssc’) and rice straw mixed in the soil (‘Smi’). In the control plots (‘Ctr’), no ash or straw was added. For each treatment 10 tons ha^{-1} of rice straw were either burned or pre-decomposed (scattered in the field for 8 weeks during the fallow period and then put into sacks at the green house where it was sprinkled with water once a day for another 3 weeks) to simulate field conditions before application to the experimental plots.

Rice seed (*Oryza sativa* L., variety NSIC Rc 222) was sown in dry seedbeds until the seedlings were 27 days old at which time they were transplanted to the plots. The rice crop was managed according to local farmers’ practices, including mechanical plowing of dry soil one month before transplanting the rice seedlings (after ca. 8 weeks fallow period), flooding and harrowing of the field two weeks before transplanting (from then on the field was kept flooded until harvesting), and leveling of the soil surface five days before transplanting.

Molluscicides (*‘Bayluscide’* - active ingredient Niclosamide) and herbicides (*‘Machete’* - active ingredient Buthachlor) were applied shortly after transplanting. Fertilizer (*‘Swire’* 14-14-14 with urea 46-0-0) was applied two times (7 and 30 days after transplanting) and no insecticides were applied during the experiment. The rice plants were harvested 82 days after transplanting.

Litterbags

In order to quantify the contribution by invertebrate decomposers to total rates of decomposition we used nylon litterbags of 15 cm × 20 cm with two different mesh sizes [47] that were filled with 10 g of air-dried, chopped rice straw (*Oryza sativa* L., variety NSIC Rc 222) and fixed to the ground by coarse nylon nets and bamboo sticks. Subsamples of the straw were retained for initial moisture and chemical analyses. The litterbags were set in the field one day after transplanting the rice seedlings. The fine-meshed litterbags had a mesh size of 20 μm × 20 μm and allowed access of microbes and part of the microfauna (e.g. fungi, bacteria, protozoa, micro-nematodes; henceforth referred to as ‘microbial decomposition’). The coarse-meshed bags had a mesh size of 5 mm × 5 mm and allowed access of most of the invertebrate groups [48]. The litter mass losses in our fine-meshed bags represented microbial driven decomposition, since microarthropods show comparatively low abundances in flooded rice agriculture [41] and therefore are assumed to have negligible influence on the decomposition process [38, 40]. Litterbags were retrieved after 25 days, 50 days and 75 days of exposure in the field. The two types of litterbags were arranged pair-wise on the soil surface with a maximum spacing of 2 cm between bags, with three replicates of one fine-meshed and one coarse-meshed litterbag per block per treatment (management practice) per retrieval time (total number of bags: 450). The litterbag pairs were randomly spread within the fields. After retrieval of the bags, soil particles, roots, and other alien plant material adhering to the straw were removed. The cleaned straw was dried at 60 °C for at least three days and weighed to the nearest centigram to calculate litter mass losses. The C and N contents of the original straw as well as retrieved straw from each litterbag were determined using an Elementar Vario EL element analyser (Elementar Analysengeräte GmbH, Hanau, Germany).

Soil fauna - Sampling and level of identification

Soil invertebrates were sampled from all 25 plots. The field sampling was carried out at 25 and 75 days after the start of the litterbag experiment. On each date, five soil core subsamples (approx. Ø 2 cm, 10 cm depth) were taken per plot for the extraction of nematodes following a modified Cobb’s decanting and sieving method [49]. The nematodes were identified to genus level and assigned to feeding groups [50]. For the mesofauna, two soil cores (approx. Ø 5 cm, 10 cm depth) were taken. Microarthropods were extracted using a MacFadyen high-gradient extractor [51], and were sorted, counted and identified to suborder or family level. The second mesofauna soil core sample was manually sieved and decanted for the extraction of *Enchytraeidae* (potworms), which were suspended in 70 % ethanol and counted. Additional cores (Ø 5 cm, 10 cm depth) were used for the analyses of abiotic soil parameters.

Aquatic fauna - Sampling and level of identification

Aquatic meso- and microfauna were taken from all 25 plots using dip nets (Ø 20 cm) of 0.8 mm mesh size. Sampling was carried out at the middle of the rice cycle (50 days after the start of the experiment) with a single sweep of 5 m length taken along the middle of each plot. The sampled invertebrates were directly transferred to 70 % ethanol, sorted and identified to family or order level. We use the term "lineage", which refers to phylogenetic groups differing in their taxonomic hierarchy in the remainder of the text, because soil and aquatic invertebrates were determined to different taxonomic levels.

Data analyses

A general linear mixed model (GLMM) Type III sum of squares (procedure MIXED, SAS 9.2) was used to analyze litter-, C- and N mass loss as well as the relative contents of C and N (split-split-plot ANOVA) in relation to *'treatment'* (crop residue management method; 5 levels within main plot), *'time'* (retrieval time of litterbags; 3 levels within sub plot), and *'mesh'* (mesh size of litterbags; 2 levels within sub-sub plot) as well as their interactions. The factors *'block'* (5 levels within main plot) and *'replicate'* (3 levels within sub plot) were considered random. Soil fauna data (split-plot ANOVA) were analyzed according to *'treatment'* and *'time'* (soil core sampling dates; 2 levels within sub plot), and also including *'block'* as a random factor. The aquatic fauna (one-way ANOVA) was analyzed in a similar way, but excluding the factor *'time'*. Post hoc Tukey's HSD tests were carried out to reveal significant differences between the respective factor levels within factors.

For analyses of community structure, average values of the two sampling dates for lineages of soil invertebrates were calculated. For comparison between sampling methods (soil core *vs*. dip net), abundances of the lineages were standardized using z-transformation. To evaluate relations between abundances of the lineages and the management methods (*'treatment'*) a redundancy analysis - RDA [52, 53] was carried out using R 2.1.4.2., package *vegan* [54]. We used this specific multivariate method, which requires linear relationships between lineages as well as between assemblages and environmental variables (Euclidean metric), because of the homogeneity in our community dataset and the short environmental gradient [55, 56]. According to Lepš and Šmilauer [57] the use of linear methods is appropriate, if the longest gradient, calculated using DCA/DCCA, is smaller than 3; in our dataset the longest gradient was 0.8.

Analyses of co-variance (ANCOVA) were used to analyze the relationships between litter mass losses and selected aquatic and soil-dwelling lineages including the same fixed and random factors as in the above described ANOVAs on litter mass losses. Lineages were included successively as covariates to reveal linear relationships of variances. Combining all independent and measured variables from our experiment, we used structural equation models (SEM) to test for direct and indirect interaction effects between observed endogenous variables (= independent variables) and exogenous predictor variables (= fixed factors).

RESULTS

Rice straw decomposition

The mean loss of litter mass in coarse-meshed litterbags was higher than in the fine-meshed bags (84 ± 0.8 % *vs.* 75 ± 0.8 % (overall mean across all treatments and retrieval times ± SE) respectively; Table 1). All tested factors as well as their two-way interactions showed highly significant effects on litter mass loss (Table 1). Mesh size had a significant effect on litter mass loss on all retrieval dates (Table 1, S3A Fig.). The mean percent litter mass loss was lower from the coarse-meshed bags (Fig 1A) retrieved after 25 days (Fig 2A) in plots with straw scattered on the surface of the field (treatment Ssc) compared to the other treatments. In both the fine- and coarse-meshed bags, retrieved later in the rice cycle, the mass loss of rice straw litter was similar across all five treatments (Fig 2A).

Except for the *treatment* × *time* interaction, N content of the retrieved rice straw litter was also affected by all tested factors and their two-way interactions (Table 1). The same applies to C contents, except that there were no significant effects of *mesh* and the *treatment x mesh* interaction (Table 1). Similar to the total litter mass loss, N and C contents were lowest in the Ssc-plots (Figs 1B and 1C). Furthermore, the difference of C contents between Ssc and the other four treatments was largest for straw in litterbags retrieved after 25 days (Fig 2C). Whereas C and N contents of straw increased with time, C/N ratios decreased (Table A in S1 File, S1B Fig). This accounts for the relatively slower loss of N compared to C during decomposition.

There was a higher increase in N content over time in coarse-meshed compared to fine-meshed litterbags, but a higher increase in C content over time in fine-meshed bags (S3B Fig. and S3C Fig.). C/N ratios also followed this pattern, with higher values for straw in the fine-meshed compared to coarse-meshed bags (S1A Fig.). When comparing the mass losses of C and N from rice straw litter retrieved from the five treatments, similar patterns emerged as for litter mass loss and relative C and N contents: firstly, there were no differences within fine-meshed bags; secondly, C and N mass loss were lower in coarse-meshed bags of treatment Ssc compared to the other four treatments; and thirdly, towards the end of the season differences between the treatments were negligible (Table B in S1 File, S4 Fig.).

Rice yield

Rice yields were affected by crop residue management practices; minimum yields were obtained from fields where the rice straw was scattered on the soil surface, but this was not significantly different from the control plots ($F_{4,16} = 3.6$, $P = 0.29$; Fig 3).

Soil and aquatic invertebrates

Crop residue treatment significantly affected the abundances of selected aquatic lineages as well as the sum of all lineages (aquatic + soil) (Table 2) with the highest abundances recorded at fields with straw amendment (treatments Ssc and Smi; Fig 4). There was no significant treatment effect on functional groups of soil invertebrates alone (Table C in S1 File). However, abundances were significantly different between the two sampling dates (S5C-G Fig.). Most mesofaunal lineages, like the *Acari*, were more abundant at the beginning of the rice cycle. Fluctuations in nematode abundances varied between the feeding guilds: plant-feeding nematodes were most abundant in the beginning, but omnivorous nematodes were most abundant towards the end of the rice cycle. There was also a significant time effect on soil parameters (soil pH & soil organic C content, Table C in S1 File, S5A Fig. and S5B Fig.), but there were no significant treatment effects.

For the RDA the variable *'treatment'* (categorical, 5 levels) was included. Based on the total variance in the dataset, the first RDA axis explained 11 % (Table D in S1 File Table; $P = 0.005$) and represented mostly the 'straw scattered' treatment (Fig 5; see also Table E in S1 File - highest absolute value at RDA 1). The second axis accounted for 5 % (Table D in S1 File; $P = 0.15$) of the total variance and was related with the 'straw mixed in' treatment (Fig 5; see also Table E in S1 File - highest absolute value at RDA 2). In total, 21 % of the variance in the dataset was explained by the four constrained RDA axes. Of this variance 52 % was explained by RDA 1 and 24 % by RDA 2 (Table D in S1 File). The factor *treatment* itself had a significant influence on the abundances of aquatic and soil invertebrates ($P = 0.02$; all results of ANOVA permutation tests are given in Table F in S1 File). Finally, we found no significant relationships between litter mass losses and fauna groups as analyses of co-variance and structural equation models did not reveal direct or indirect interaction effects.

Table 1. The effects of ‘*treatment*’, ‘*time*’ and ‘*mesh*’ and their interactions on litter mass loss of rice straw and the N and C contents of the retrieved straw using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Factors	Litter mass loss (%)			N content (%)			C content (%)		
	Df	F	*P*	Df	F	*P*	Df	F	*P*
treatment	4,16	6.31	**0.003**	4,16	3	**0.05**	4,16	23.50	**< .0001**
time	2,187	2053	**< .0001**	2,187	579	**< .0001**	2,187	562	**< .0001**
mesh	1,206	652	**< .0001**	1,206	266	**< .0001**	1,206	0.01	0.91
treatment × *time*	8,187	8.47	**< .0001**	8,187	1.52	0.15	8,187	4.56	**< .0001**
treatment × *mesh*	4,206	7.78	**< .0001**	4,206	12	**< .0001**	4,206	0.65	0.63
mesh × *time*	2,206	61.5	**< .0001**	2,206	24.8	**< .0001**	2,206	36.2	**< .0001**
treatment × *mesh* × *time*	8,206	1.27	0.26	8,206	1.18	0.31	8,206	2.23	**0.03**

Factor ‘*treatment*’ represents the five different management practices (Asc, Ami, Ssc, Smi, Ctr; for abbreviations see Fig 1), the factor ‘*time*’ is the effect of the three different time periods for which the bags were left in the fields (25d, 50d, 75d), and factor ‘*mesh*’ the two mesh sizes (5 mm and 20 µm) used in every plot. The model also includes the random effects of the factors ‘*block*’ and ‘*replicate*’; these two factors and their interactions are not shown.

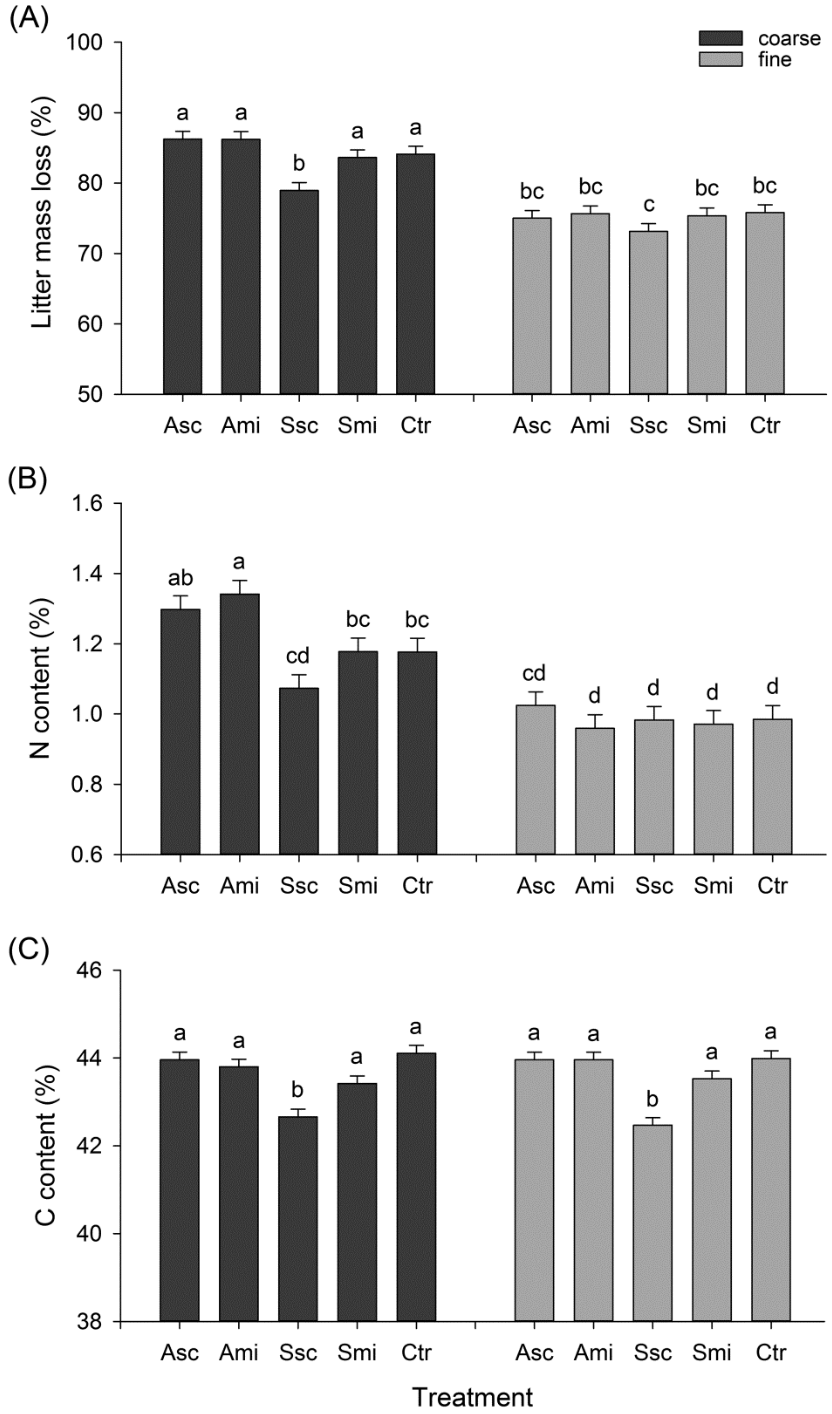

Fig 1. Litter mass loss, C content, N content: mesh size × treatment. Percent litter mass loss (A), N content (B) and C content (C) (means + standard error SE) of rice straw retrieved after the five treatments in coarse-meshed (decomposition by invertebrates and microorganisms) and fine-meshed (decomposition by microorganisms) litterbags. Different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). Values of the original straw (= *time 0d*): N = 0.6 %, C = 36.8 %. Treatment abbreviations: 'Asc' - ash of burned rice straw scattered on the field, 'Ami' - ash of burned rice straw mixed into the soil, 'Ssc' - rice straw scattered on the field, 'Smi' - rice straw mixed into the soil, 'Ctr' - control (no ash or straw added).

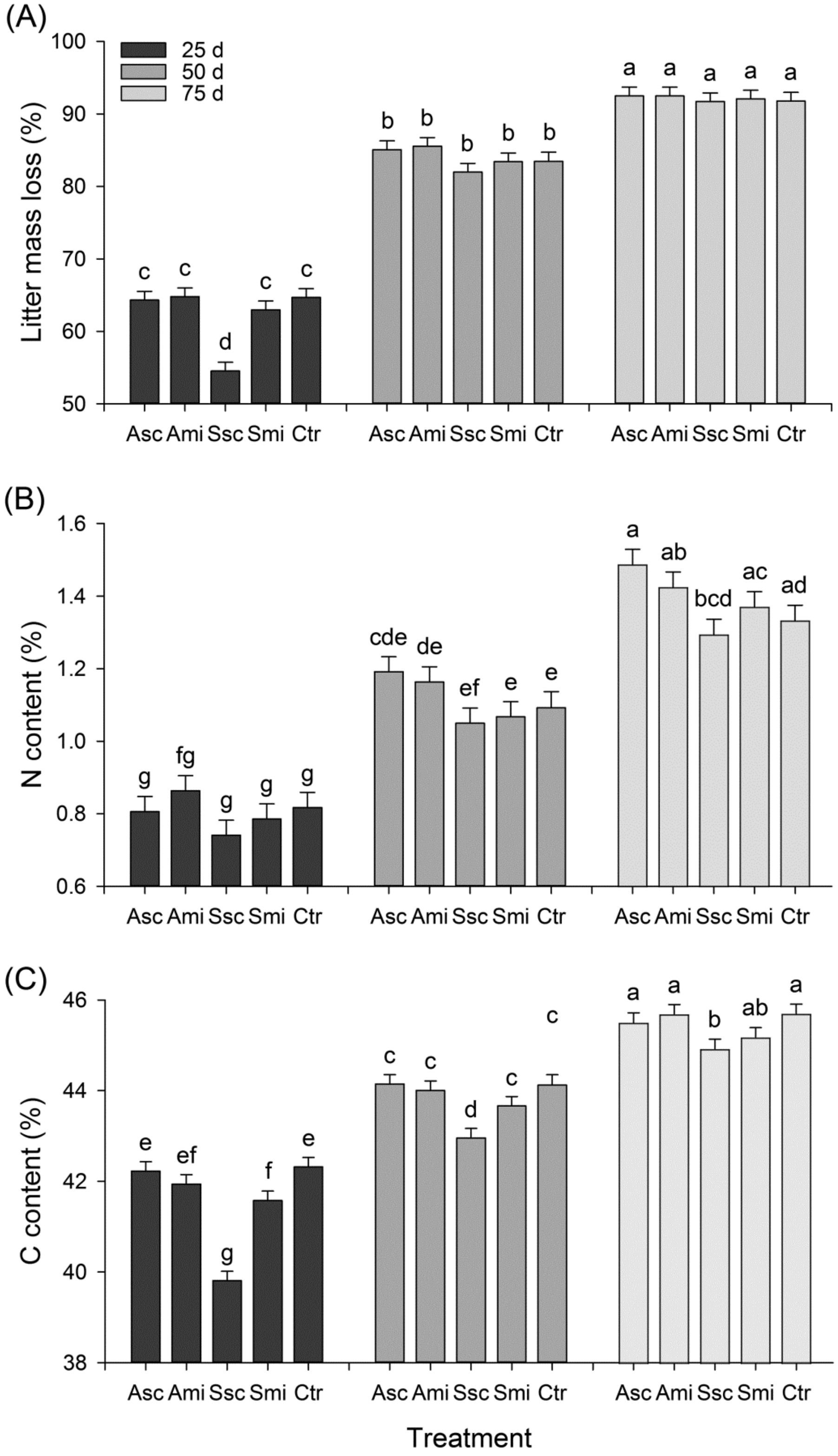

Fig 2. Litter mass loss, C content, N content: treatment × time. Percent litter mass loss (A), N content (B) and C content (C) (means + SE) of rice straw litter retrieved from the five treatments at three points in time. Different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). Values of the original straw (= *time 0d*): N = 0.6 %, C = 36.8 %. For abbreviations see Fig 1.

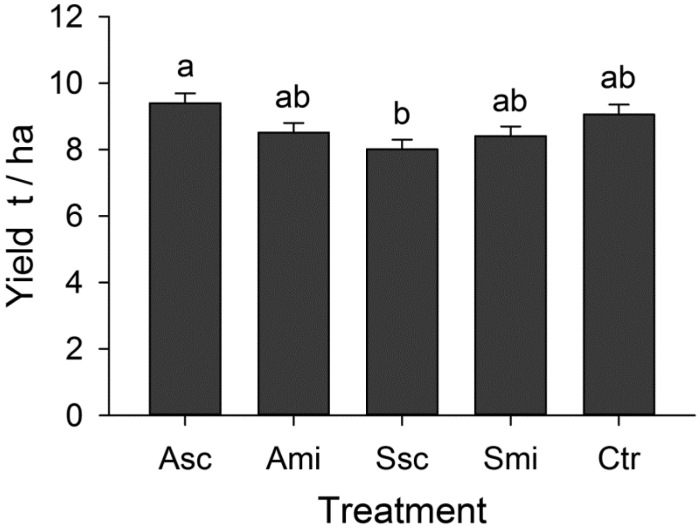

Fig 3. Rice yields. Yields per *'treatment'* calculated from an adjusted grain weight at 14 % moisture content (means + SE); different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). For abbreviations see Fig 1.

Table 2. The effect of ‘*treatment*’ on selected aquatic fauna groups and the sum of all lineages using a GLMM type III sum of squares. Error df = 16; significant effects are indicated in bold font.

Factor	Annelida abundance (sqrt)			Aquatic Nematoda abundance			Cladocera abundance		
	Df	F	*P*	Df	F	*P*	Df	F	*P*
treatment	4	3.48	**0.03**	4	4.12	**0.02**	4	4.68	**0.01**
	Coleoptera abundance			Aquatic fauna abundance (sqrt)			Abundance - all lineages (ln)		
	Df	F	*P*	Df	F	*P*	Df	F	*P*
treatment	4	7.7	**0.001**	4	4.64	**0.01**	4	5.09	**0.01**

Factor ‘*treatment*’ represents the five different management practices (Asc, Ami, Ssc, Smi, Ctr; for abbreviations see Fig 1). “Abundance - all lineages” refers to the total numbers of aquatic and soil invertebrates. The model also includes the random effect of the factor ‘*block*’; which is not shown; ‘sqrt’ - data square root transformed, ‘ln’ - data $\log_e$ transformed.

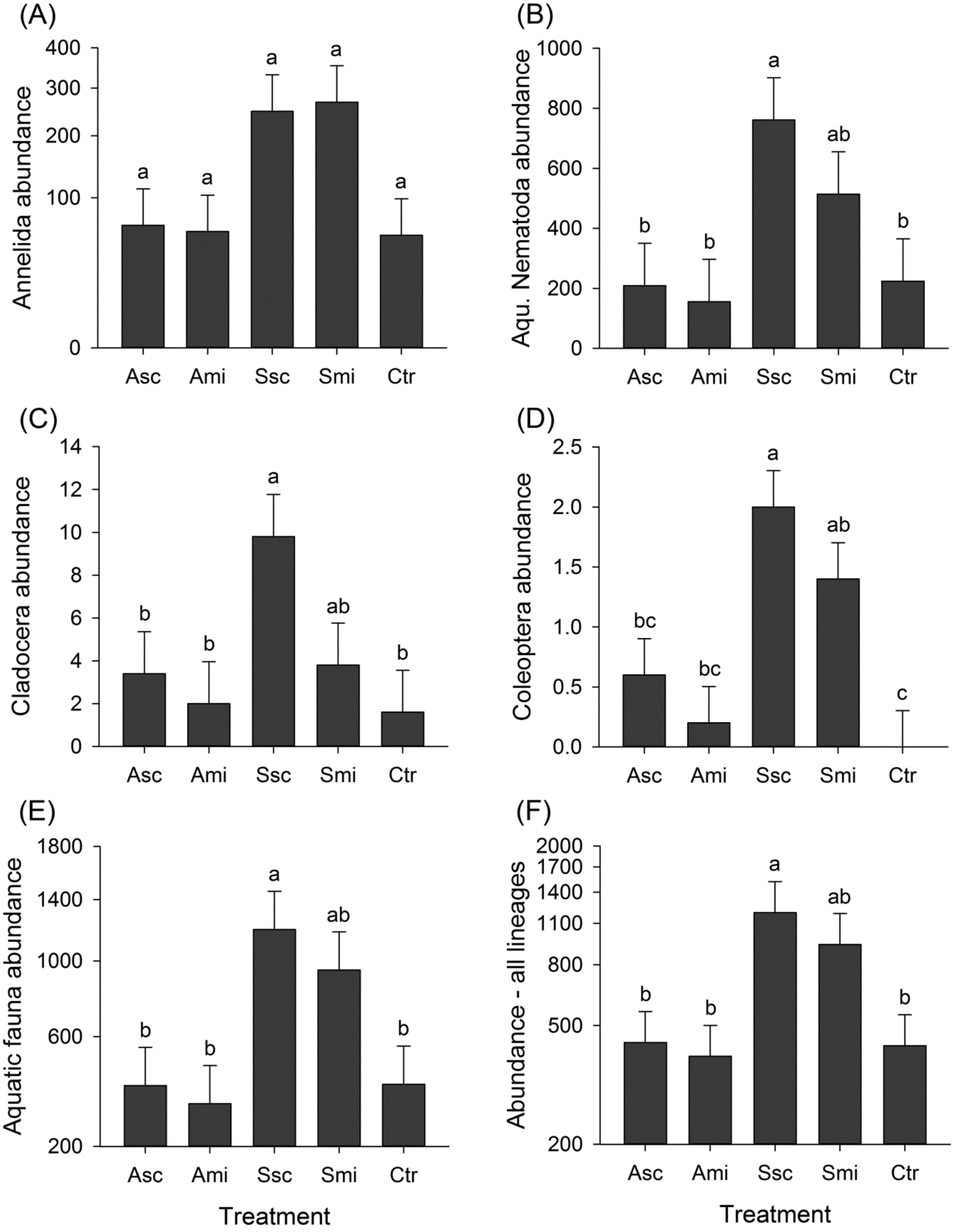

Fig 4. Abundance of aquatic fauna. Abundances of aquatic fauna groups and all lineages per '*treatment*' (number of individuals). Panel (E) shows the sum of all aquatic fauna samples and panel (F) shows the total numbers of aquatic fauna together with soil fauna (means + SE); different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). For the number of annelids the post-hoc test revealed no significant differences in means. For abbreviations see Fig 1.

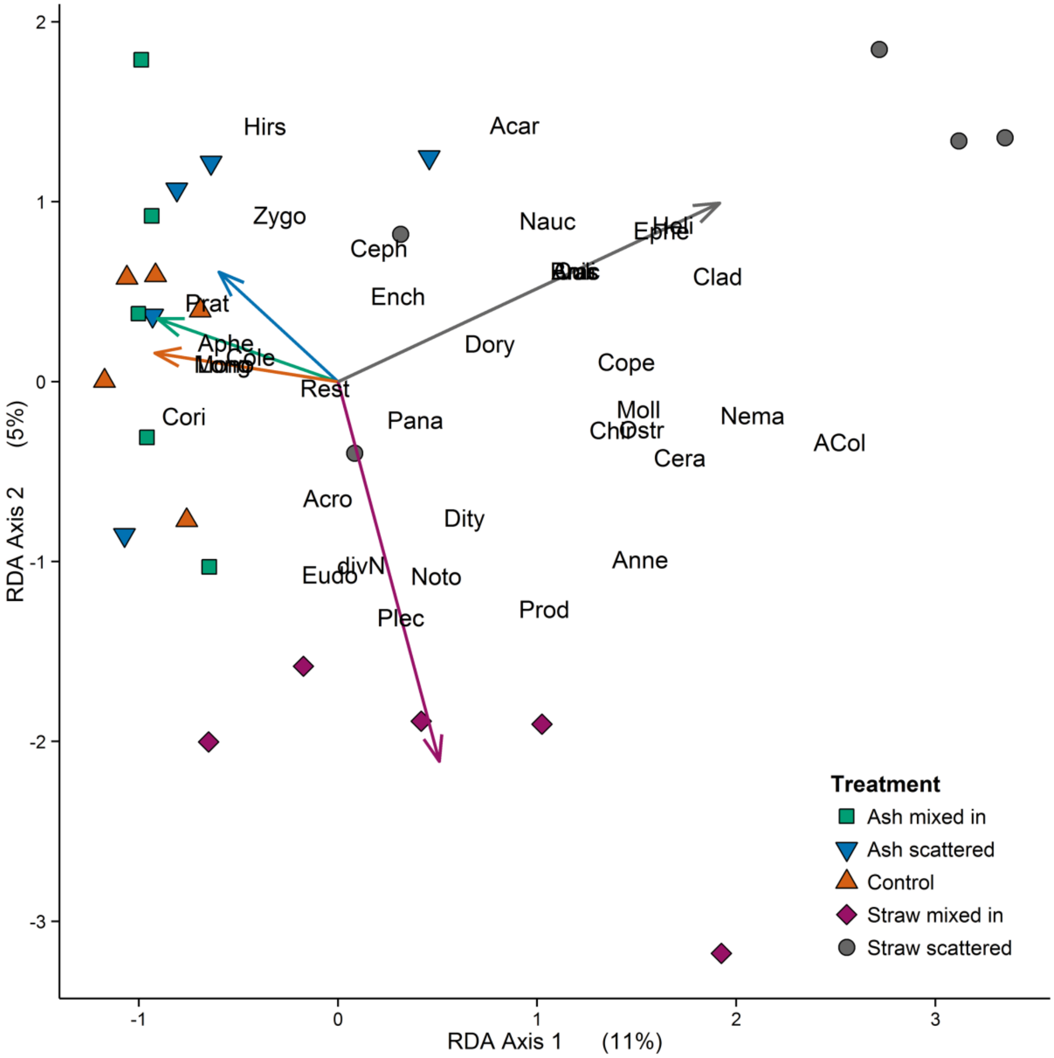

Fig 5. RDA plot including all lineages. Euclidean distance biplot based on a redundancy analysis (RDA); fauna groups of aquatic and soil samples are represented by their 4-letter-abbreviations (see below); arrows refer to the five levels of the environmental variable '*treatment*'; and site scores are shown with different shapes and colors depending on their treatment affiliation. Axis 1 explains proportionally 11 % ($P \leq 0.01$) of the variation in the dataset; Axis 2 accounts for 5 % (*n.s.*) of the variation.

Abbreviations of animal lineages: *aquatic fauna:* ACol - Coleoptera Imagos, Anis - Anisoptera Larvae, Anne - Annelida, Brac - Brachycera Larvae, Cera - Ceratopogonidae Larvae, Chir - Chironomidae Larvae, Clad - Cladocera, Cole - Coleoptera Larvae, Cope - Copepoda, Cori - Corixidae, Culi - Culicidae Larvae, divN - Nematocera Larvae (except for Chironomidae and Culicidae), Ephe - Ephemeroptera Larvae, Moll - Mollusca, Nauc - Naucoridae, Nema - Nematoda, Noto - Notonectidae, Ostr - Ostracoda, Plec - Plecoptera Larvae, Zygo - Zygoptera Larvae; *soil mesofauna:* Acar - Acari, Ench - Enchytraeidae, Rest - remaining (not specified) invertebrates from soil samples; *soil nematodes:* Acro - Acrobeles spp., Ceph - Cephalobus spp., Pana - Panagrolaimus spp., Plet - Plectus spp. (all bacterial-feeding), Aphe - Aphelenchoides spp. (hyphal-feeding), Dity - Ditylenchus spp. (plant-associated), Heli - Helicotylenchus spp., Hirs - Hirshamanniella spp., Long - Longidorus spp., Prat - Pratylenchus spp. (all plant-feeding), Dory - Dorylaimus spp., Eudo - Eudorylaimus spp., Prod - Prodorylaimus spp. (all omnivorous), Mono - Monochus spp. (predator).

DISCUSSION

Rice straw decomposition

The present study demonstrates the importance of invertebrate decomposers as ecosystem engineers for sustainable agricultural practices in flooded rice production systems. The rate of decomposition is known to be influenced by a variety of abiotic and biotic factors [3, 20]. According to Singh et al. [18] three main factors are important for efficient residue decomposition in rice-based cropping systems: (1) crop residue factors (like C/N ratios and lignin concentration), (2) edaphic factors (soil properties like moisture content), and (3) management factors. For a long-term sustainable improvement of management practices in paddy fields, it is crucial to understand the ways in which these often interacting factors influence the decomposition of rice straw by invertebrates.

In our experiment, invertebrates contributed to rice straw decomposition as demonstrated by the higher losses of litter biomass from coarse-meshed litterbags compared to fine-meshed ones. This pattern corroborates the results of several previous field studies (e.g. [10, 38]) and supports our first hypothesis that invertebrates contribute to the mass loss of rice straw in paddy fields. The few previous studies dealing with litter decomposition by invertebrates have mostly been conducted in “true” farmers' rice fields, but not under the controlled and comparable conditions as provided at our experimental sites. In general, it may be reasonably assumed that the straw bundled in our litterbags created microsites with a comparably low redox potential that decreased microbial decomposition activity [58]. This implies that our decomposition rates are likely underestimated and that microbial decomposition of dispersed straw is likely higher than that measured in our litterbags. Nevertheless, microbial decomposition of organic matter is less efficient under the anaerobic conditions (e.g. [58]) prevalent in flooded rice fields. In such environments, invertebrate decomposers will ensure sufficient nutrient precipitation from plant residues.

One important step during invertebrate-driven decomposition is straw shredding, which increases the surface area of the rice straw, and therefore the residue-soil contact, and creates a more stable and favorable environment for microbial decomposition [18, 59]. Residue incorporation enhances this effect [18] as is reflected in our results: Litter decomposition with invertebrates (litter mass loss in coarse-meshed litterbags) was significantly faster in fields with rice straw incorporated into the soil compared to fields with rice straw scattered on the field surface. No significant response of solely microbial decomposition (litter mass loss in fine-meshed bags) on management practices was detectable, which indicates that management practices primarily affect decomposition by invertebrates. The process of rice straw decomposition in paddies can be divided into two phases with a rapid phase of decomposition at the beginning (due to leaching and the presence of easily degradable organic C in fresh residues) followed by a slower phase [60]. We found a similar pattern in our experiment (highest litter mass losses after 25 days of incubation), which supports our fourth hypothesis that the abundances of functional groups of invertebrates and their relative contribution to decomposition vary over time with stronger effects at the beginning of the season. It may also explain why differences in litter mass losses between management methods leveled off towards the end of the rice cycle.

It is known that decomposition is related to the C and N contents of plant residues [61]. At the very beginning of the decomposition process, a strong decrease in relative C content due to mineralization processes by microorganisms is common [62]. However, C and N contents in the rice straw litter steadily increased during the time of our experiment which was most likely due to a high leaching of other soluble components, like silicon and potassium [63, 64]. Klotzbücher et al. [46] showed that rice straw from the Laguna region in the Philippines (which we used in our litterbags) has particularly high silicon concentrations, which can amount to nearly five percent of total rice straw dry mass. The reduction of silicon is very fast in paddy fields resulting in higher silicon losses during decomposition compared to C and N mass loss. We found similar changes in C concentration of straw retrieved from both litterbag types which suggests a primarily microbial-driven C-breakdown. In contrast, N contents in the straw differed between fine- and coarse-meshed litterbags and reflected the patterns of the above described litter mass losses: No differences between treatments in straw from fine-meshed bags and generally higher N contents in straw from coarse-meshed bags with lowest values in fields with Ssc treatment. Higher N concentration in the litter may be due to higher fungal biomass [65] which would increase N concentrations creating more attractive conditions for detritivores. This may explain the higher litter mass losses in bags where they had access. This idea is supported by the results of several studies (e.g. [65, 66, 67]) which have reported a positive correlation between decomposition rates and the N contents of plant materials.

Although rice straw is a low-quality resource for decomposers (see Introduction), decomposition rates in rice paddies are rather high. Therefore, N content of the litter is not the only important determinant of litter decomposition rates in wet-rice agriculture. Tian et al. [61] reported that the role of soil fauna is relatively greater in the decomposition of low-quality litter: High C/N ratios as well as high lignin and polyphenol contents decrease the ability of microorganisms to decompose straw. Microbial-driven decomposition is additionally slowed by the anaerobic conditions of flooded rice fields. In fields with ash amendment and with straw mixed into the soil, a lower availability of decomposable plant material in the aquatic phase (where litterbags were set-out) could have led our litterbags to behave as “decomposer baits” leading to a faster colonization of the litterbags by detritivores at the beginning of the experiment. This assumption is supported by the convergence in the loss of rice litter for all five treatments towards the end of the season. In contrast, C and N contents maintained lower levels in the litterbag straw of fields where the rice straw was scattered on the soil surface.

Invertebrates

Several studies have demonstrated that aquatic invertebrates in rice fields cover the entire spectrum of the freshwater fauna ([36] and references therein). The decomposer fauna in tropical soils consists of morphologically and behaviorally diverse lineages [4] where macro-invertebrates mainly contribute to litter decomposition by burying and shredding of plant material. The positive effects of straw on invertebrate abundances with no effect on the diversity of aquatic or soil invertebrates in the present study is consistent with the findings of Schneider et al. [43] and Hagen et al. [42]. Although the differences between management methods were statistically significant only for the aquatic lineages, the abundances of soil-dwelling lineages showed similar trends in our study. Abundances were consistently highest at plots where straw was scattered on the field surface followed by the fields where the straw was incorporated into the soil. This positive reaction of meso- and macro-invertebrates to straw scattering supports our third hypothesis that the mode of residue application to fields will favor different groups of invertebrates. This is further supported by the findings of Friebe and Henke [44] and Reddy et al. [68], who recorded higher faunal abundances in fields with lower tillage intensity. In contrast, Singh et al. [18] suggested that the incorporation of crop residues into the soil increased populations of all types of macro- and microorganisms in rice fields in India. Whether incorporated or not, the use of rice straw as a fertilizer in irrigated rice cropping systems is beneficial for aquatic and soil invertebrates. We found no positive correlation between the abundance of meso-invertebrates and the decomposition rate. However, such a relationship has been reported by Lekha et al. [1]. Moreover, litter mass losses and the abundances of aquatic fauna showed contrasting patterns in their treatment responses. More long-term experiments will be essential to reveal the relations of invertebrates and their decomposition activity.

Even though the abundance of invertebrates was highest at plots with straw scattered on the field surface, rice plants at these plots produced the lowest yields. Different and partly contradicting short-term effects of practices of crop residue management on rice yields underline the fact that such processes may not manifest within one rice cycle. Xu et al. [69] found no effect of straw amendment on yields in the first season during their experiments, regardless of whether the fields were tilled or not. Long-term experiments by Samra et al. [28], Singh et al. [70] and Thuy et al. [31] also revealed that several crop cycles with continuous residue application are necessary to gain the maximum benefits of straw incorporation.

Despite explaining just a small amount of variance, multivariate analyses indicated that the community composition and abundances of invertebrate lineages differed significantly between our five treatments (straw or ash scattered or incorporated, and control). The graphical illustration of the RDA results revealed a clear separation and clustering of plots with straw treatments. These two straw management methods accounted for the highest amount of variation among all five treatments. Furthermore, their treatment arrows are nearly orthogonal to each other indicating a strong separation of the invertebrate assemblages at these sites. The positioning of the lineages relative to the straw-treatment-arrows shows no ecologically meaningful pattern. However, there are still some obvious trends. Some lineages, like nematodes, cluster primarily in the direction of the arrow representing the straw incorporated management method, while many aquatic lineages seem to favor fields with straw scattered onto the soil surface. Half of these aquatic lineages comprise mainly small plant-, detritus- and bacterial-feeding or omnivorous lineage types (like e.g. *Cladocera* or larvae of *Culicidae* and *Brachycera*); the other half consists of their predators (*Naucoridae*, *Anisoptera* larvae etc.). Thus, straw on the soil surface of rice fields seems to attract small aquatic invertebrates as it provides energetic resources and refuge from predators [71]; this in turn also attracts predatory insects due to an increased prey abundance [42].

Studies like ours will help to unravel the complex mechanisms and interacting effects of faunal abundance, decomposer activity and strategies of crop residue management in tropical flooded rice ecosystems. The next step is the synchronization of plant demand with N fertilization and nutrient release from rice straw residues to reduce the amount of artificial fertilizers that are applied in modern agriculture [20, 31-33], and additionally, to decrease rice straw burning and its subsequent contribution to climate change through air pollutants [72-74].

CONCLUSIONS

Linking farmers' interests with a sustainable improvement of agricultural practices in compliance with nature conservation is one of the future challenges to stabilize or even increase yields while preserving biodiversity and natural landscape structures. In our study, we demonstrated that invertebrate decomposers contribute substantially to decomposition processes in flooded rice agriculture indicating potential effects on soil fertility and site productivity. Sustainable crop residue management strategies should consider invertebrates when using straw to improve soil conditions. We showed that altering residue management practices prior to cropping significantly influences the litter decomposing activity of invertebrates during the first rice cycle, but we found no effects on microbial-driven decomposition rates. Increasing the rice straw availability in paddy fields, during the aquatic phase as well as in the soil, positively affected the abundances of aquatic and soil fauna groups. Future long-term studies should particularly focus on revealing linkages between litter decomposition by invertebrates and their abundances to evaluate in more detail how crop residue management practices can contribute to the maintenance of ecosystem services provided by invertebrate decomposers in flooded rice ecosystems.

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REFERENCES OF CHAPTER 3

1. Lekha A, Chopra G, Gupta SR. Role of soil fauna in decomposition of rice and sorghum straw. Proc Indian Acad Sci. 1989;98(4):275-84.
2. Dungait JAJ, Hopkins DW, Gregory AS, Whitmore AP. Soil organic matter turnover is governed by accessibility not recalcitrance. Global Change Biology. 2012;18(6):1781-96.
3. García-Palacios P, Maestre FT, Kattge J, Wall DH. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecol Lett. 2013;16(8):1045-53.
4. Beare MH, Reddy MV, Tian G, Srivastava SC. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of decomposer biota. Applied Soil Ecology. 1997;6:87-108.
5. Wolters V. Soil Invertebrates - Effects on Nutrient Turnover and Soil Structure - A Review. Zeitschrift für Pflanzenernährung und Bodenkunde. 1991;154(6):389-402.
6. Lavelle P, Dangerfield M, Fragoso C, Eschenbrenner V, Lopez-Hernandez D, Pashanasi B, et al. The relationship between soil macrofauna and tropical soil fertility. In: Woomer PL, Swift MJ, editors. The Biological Management of Tropical Soil Fertility. Chichester, UK: Wiley; 1994. p. 137-69.
7. Anderson JM. Spatiotemporal effects of invertebrates on soil processes. Biology and Fertility of Soils. 1988;6(3):216-27.
8. Powell JR, Craven D, Eisenhauer N. Recent trends and future strategies in soil ecological research—Integrative approaches at Pedobiologia. Pedobiologia. 2014;57(1):1-3.
9. Ferreira V, Encalada AC, Graça MAS. Effects of litter diversity on decomposition and biological colonization of submerged litter in temperate and tropical streams. Freshwater Science. 2012;31(3):945-62.
10. Schmidt A, Auge H, Brandl R, Heong KL, Hotes S, Settele J, et al. Small-scale variability in the contribution of invertebrates to litter decomposition in tropical rice fields. Basic and Applied Ecology. 2015. doi: http://dx.doi.org/10.1016/j.baae.2015.01.006.
11. Schulze ED, Mooney HA. Biological Diversity and Ecosystem Functioning. New York: Springer; 1993.
12. Anderson JM. Functional attributes of biodiversity in land use systems. In: Greenland DJ, Szaboics I, editors. Soil Resilience and Sustainable Land Use. Warlingham, UK: CAB International; 1994. p. 267-89.
13. Eisenhauer N, Schädler M. Inconsistent impacts of decomposer diversity on the stability of aboveground and belowground ecosystem functions. Oecologia. 2011;165(2):403-15.
14. de Vries FT, Thébault E, Liiri M, Birkhofer K, Tsiafouli MA, Bjørnlund L, et al. Soil food web properties explain ecosystem services across European land use systems. Proceedings of the National Academy of Sciences. 2013;110(35):14296-301.

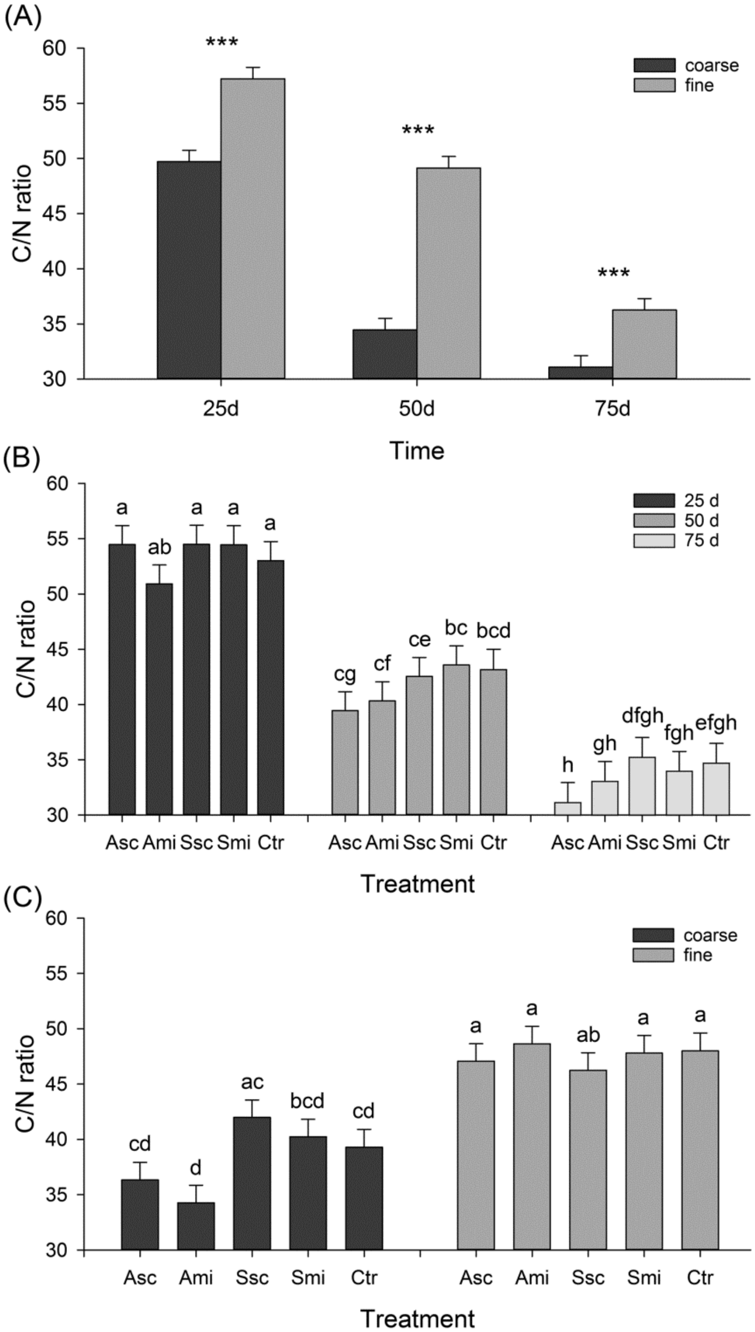
15. Tian G, Brussaard L, Kang BT. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions: effects on soil fauna. Soil Biology & Biochemistry. 1993;25(6):731-7.
16. Witkamp M, Ausmus BS. Processes in decomposition and nutrient transfer in forest ecosystems. In: Anderson JM, Macfadyen A, editors. The Role of Terrestrial and Aquatic Organisms in Decomposition Processes. Oxford: Blackwell Scientific; 1976. p. 375-96.
17. Khandaker AH, Horiuchi T, Miyagawa S. Effects of Powdered Rice Chaff on Growth and Yield of Rice Under Different Soil pH Conditions. Communications in Soil Science and Plant Analysis. 2004;35(9-10):1469-84.
18. Singh Y, Singh B, Timsina J. Crop residue management for nutrient cycling and improving soil productivity in rice-based cropping systems in the tropics. Advances in Agronomy. 2005;85.
19. Riutta T, Slade EM, Bebber DP, Taylor ME, Malhi Y, Riordan P, et al. Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. Soil Biology and Biochemistry. 2012;49:124-31.
20. Villegas-Pangga G, Blair G, Lefroy R. Measurement of decomposition and associated nutrient release from straw (Oryza sativa L.) of different rice varieties using a perfusion system. Plant and Soil. 2000;223(1-2):1-11.
21. Heal OW, Anderson JM, Swift MJ. Plant residue quality and decomposition: An historical overview. In: Cadisch G, Giller KE, editors. Driven by nature: plant Residue Quality and Decomposition. Cambridge: CAB International; 1997. p. 3-30.
22. Kowalenko CG, Ivarson KC, Cameron DR. Effects of moisture content, temperature and nitrogen fertilization on carbon dioxide evolution from field soils. Soil Biology & Biochemistry. 1978;10:417-23.
23. Bollen WB. Mulches and soil conditioners: carbon and nitrogen in farm and forest products. Agric Food Chain. 1953;1:379-81.
24. Canhoto C, Graça MAS. Food value of introduced eucalypt leaves for a Mediterranean stream detritivore: Tipula lateralis. Freshwater Biology. 1995;34(2):209-14.
25. Swan CM, Palmer MA. Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. Oecologia. 2006;147(3):469-78.
26. Schädler M, Jung G, Auge H, Brandl R. Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. Oikos. 2003;103:121-32.
27. Fairhurst T, Witt C, Buresh R, Dobermann A. Rice: A practical guide to nutrient management. 2nd ed. Los Banos, Philippines: International Rice Research Institute, International Plant Nutrition Institute and International Potash Institute; 2007.
28. Samra JS, Singh B, Kumar K. Managing crop residues in the rice-wheat system of the Indo-Gangetic plain. In: Ladha JK, editor. Improving the productivity and sustainability of rice–wheat systems: Issues and impacts: ASA Spec. Publ. 65. ASA, CSSA, and SSSA, Madison, WI.; 2003.

29. Dobermann A, Fairhurst T. Rice straw management. Better Crops Int. 2002;16(1):7-11.
30. Singh Y, Gupta RK, Jagmohan S, Gurpreet S, Gobinder S, Ladha JK. Placement effects on rice residue decomposition and nutrient dynamics on two soil types during wheat cropping in rice–wheat system in northwestern India. Nutrient Cycling in Agroecosystems. 2010;88(3):471-80.
31. Thuy NH, Shan Y, Singh B, Wang K, Cai Z, Singh Y, et al. Nitrogen Supply in Rice-Based Cropping Systems as Affected by Crop Residue Management. Soil Sci Soc Am J. 2008;72(2):514-23.
32. Bird JA, Horwath WR, Eagle AJ, van Kessel C. Immobilization of fertilizer nitrogen in rice: Effects of straw management practices. Soil Science Society of America Journal. 2001;65:1143-52.
33. Eagle AJ, Bird JA, Hill JE, Horwath WR, van Kessel C. Nitrogen dynamics and fertilizer use efficiency in rice following straw incorporation and winter flooding. Agronomy Journal. 2001;93:1346-54.
34. Li X, Wu J, Zhu H, Wang Y. Effect of straw returning on crop yield and soil fertility (In Chinese, with English abstract). Journal of Anhui Agricultural Sciences. 2003;31:870-1.
35. Cucu MA, Said-Pullicino D, Maurino V, Bonifacio E, Romani M, Celi L. Influence of redox conditions and rice straw incorporation on nitrogen availability in fertilized paddy soils. Biology and Fertility of Soils. 2014;50(5):755-64.
36. Bambaradeniya CNB, Amarasinghe FP. Biodiversity associated with the rice field agroecosystem in Asian countries: A brief review. Working Paper 63. Colombo, Sri Lanka: International Water Management Institute;2003.
37. Fernando CH, editor. Ricefield ecosystems: a synthesis. Tropical Ecology and Development: Proceedings of the 5th Int. Symp. of Tropical Ecology; 1979 16-21 Apr; Kuala Lumpur: International Society of Tropical Ecology. 1980.
38. Widyastuti R. Soil fauna in rainfed paddy field ecosystems: their role in organic matter decomposition and nitrogen mineralization. Ecology and Development Series Band 3. Cuvillier Verlag, Göttingen. 2002.
39. Chaudhury J, Mandal UK, Sharma KL, Ghosh H, Mandal B. Assessing Soil Quality Under Long-Term Rice-Based Cropping System. Communications in Soil Science and Plant Analysis. 2005;36(9-10):1141-61.
40. Liang W, Li Q, Jiang Y, Neher DA. Nematode faunal analysis in an aquic brown soil fertilised with slow-release urea, Northeast China. Applied Soil Ecology. 2005;29(2):185-92.
41. Cancela da Fonseca JP, Sarkar S. Soil microarthropods in two different managed ecological systems (Tripura, India). Applied Soil Ecology. 1998;9(1–3):105-7.
42. Hagen EM, McCluney KE, Wyant KA, Soykan CU, Keller AC, Luttermoser KC, et al. A meta-analysis of the effects of detritus on primary producers and consumers in marine, freshwater, and terrestrial ecosystems. Oikos. 2012;121(10):1507-15.

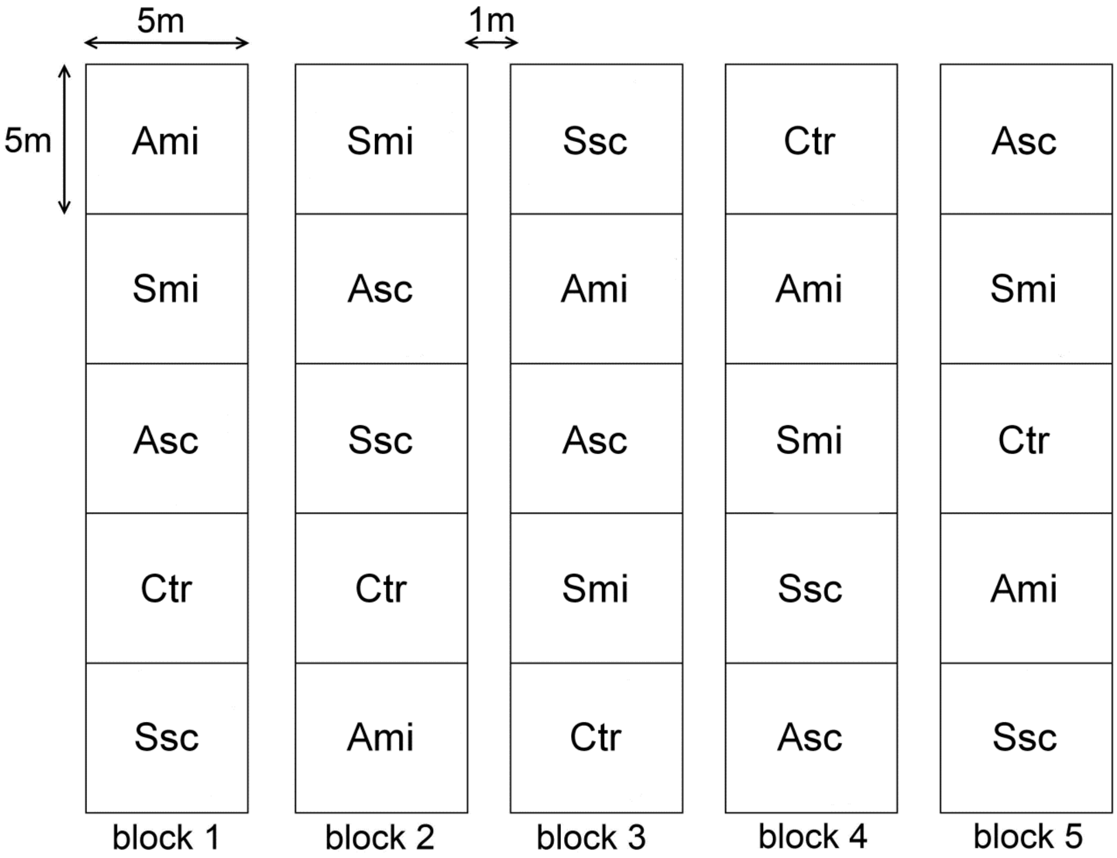
43. Schneider K, Christman MC, Fagan WF. The influence of resource subsidies on cave invertebrates: results from an ecosystem-level manipulation experiment. Ecology. 2010;92(3):765-76.
44. Friebe B, Henke W. Soil fauna and their straw decomposition capacity on reduced tillage. Z Kulturtech Landentw. 1991;32:121-6.
45. Settele J, Kühn I, Klotz S, Arida G, Bergmeier E, Burkhard B et al. A cultural landscapes and ecosystems services in south-east Asia – The LEGATO-project. Basic and Applied Ecology. 2015. In press.
46. Klotzbücher T, Marxen A, Vetterlein D, Schneiker J, Türke M, van Sinh N, et al. Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. Basic and Applied Ecology. 2015. doi: http://dx.doi.org/10.1016/j.baae.2014.08.002.
47. Bokhorst S, Wardle DA. Microclimate within litter bags of different mesh size: Implications for the ‘arthropod effect’ on litter decomposition. Soil Biology and Biochemistry. 2013;58:147-52.
48. Tian G, Kang BT, Brussaard L. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions - decomposition and nutrient release. Soil Biology & Biochemistry. 1992;24(10):1051-60.
49. Cobb NA. Estimating the Nema Population of Soil. U.S. Department of Agriculture, Washington DC, USA: Bureau of Plant Industry; 1918. 48 p.
50. Yeates GW, Bongers T, De Goede RGM, Freckman DW, Georgieva SS. Feeding habits in soil nematode families and genera - an outline for soil ecologists. Journal of nematology. 1993;25(3):315.
51. MacFadyen A. Improved Funnel-Type Extractors for Soil Arthropods. Journal of Animal Ecology. 1961;30(1):171-84.
52. van den Wollenberg AL. Redundancy analysis an alternative for canonical correlation analysis. Psychometrika. 1977;42(2):207-19.
53. Rao CR. The use and interpretation of principal component analysis in applied research. Sankhyā: The Indian Journal of Statistics, Series A. 1964;26:329-58.
54. Oksanen J, Kindt R, Legendre P, O’Hara B, Stevens MHH, Oksanen MJ, et al. The vegan package. Community ecology package. 2007.
55. Leyer I, Wesche K. Multivariate Statistik in der Ökologie - Eine Einführung. Berlin Heidelberg New York: Springer; 2007.
56. Dormann CF, Kühn I. Angewandte Statistik für die biologischen Wissenschaften. 2nd ed. Helmholtz Zentrum für Umweltforschung-UFZ. 2008.
57. Lepš J, Šmilauer P. Multivariate Analysis of Ecological Data Using CANOCO. New York: Cambridge University Press; 2003.
58. Kögel-Knabner I, Amelung W, Cao Z, Fiedler S, Frenzel P, Jahn R, et al. Biogeochemistry of paddy soils. Geoderma. 2010;157(1-2):1-14.

59. Cogle AL, Strong WM, Saffigna PG, Ladd JN, Amato M. Wheat straw decomposition in subtropical Australia. II. Effect of straw placement on decomposition and recovery of added ^{15}N-urea. Australian Journal of Soil Research. 1987;25(4):481-90.
60. Lu Y, Watanabe A, Kimura M. Carbon dynamics of rhizodeposits, root- and shoot-residues in a rice soil. Soil Biology and Biochemistry. 2003;35(9):1223-30.
61. Tian G, Brussaard L, Kang BT. An index for assessing the quality of plant residues and evaluating their effects on soil and crop in the (sub-)humid tropics. Applied Soil Ecology. 1995;2:25-32.
62. Miller C. Understanding the carbon-nitrogen ratio. Acres USA. 2000;30(4):20-1.
63. Saha PK, Miah MAM, Hossain ATMS, Rahman F, Saleque MA. Contribution of rice straw to potassium supply in rice-fallow-rice cropping pattern. Bangladesh Journal of Agricultural Research. 2009;34(4):633-43.
64. Christensen BT. Wheat and barley straw decomposition under field conditions: Effect of soil type and plant cover on weight loss, nitrogen and potassium content. Soil Biology and Biochemistry. 1985;17(5):691-7.
65. Perez J, Galan J, Descals E, Pozo J. Effects of fungal inocula and habitat conditions on alder and eucalyptus leaf litter decomposition in streams of northern Spain. Microbial ecology. 2014;67(2):245-55.
66. Alexander M. Introduction to soil microbiology. New York: John Wiley & Sons.; 1977.
67. Martinez A, Larranaga A, Perez J, Descals E, Pozo J. Temperature affects leaf litter decomposition in low-order forest streams: field and microcosm approaches. FEMS Microbiol Ecol. 2014;87(1):257-67.
68. Reddy MV, Reddy VR, Yule DF, Cogle AL, George PJ. Decomposition of straw in relation to tillage, moisture, and arthropod abundance in a semi-arid tropical Alfisol. Biology and fertility of soils. 1994;17:45-50.
69. Xu Y, Nie L, Buresh RJ, Huang J, Cui K, Xu B, et al. Agronomic performance of late-season rice under different tillage, straw, and nitrogen management. Field Crops Research. 2010;115(1):79-84.
70. Singh B, Bronson KF, Singh Y, Khera TS, Pasuquin E. Nitrogen-15 balance as affected by rice straw management in a rice–wheat rotation in northwest India. Nutrient Cycling in Agroecosystems. 2001;59:227-37.
71. Moore JC, Berlow EL, Coleman DC, Ruiter PC, Dong Q, Hastings A, et al. Detritus, trophic dynamics and biodiversity. Ecology Letters. 2004;7(7):584-600.
72. Levine JS. Biomass Burning and Global Change: Remote sensing, modeling and inventory development, and biomass burning in Africa: MIT Press; 1996.
73. Andreae MO, Crutzen PJ. Atmospheric aerosols: Biogeochemical sources and role in atmospheric chemistry. Science. 1997(276):1052-8.
74. Wassmann R, Lantin RS, Neue HU, Buendia LV, Corton TM, Lu Y. Characterization of Methane Emissions from Rice Fields in Asia. III. Mitigation Options and Future Research Needs. Nutrient Cycling in Agroecosystems. 2000;58(1-3):23-36.

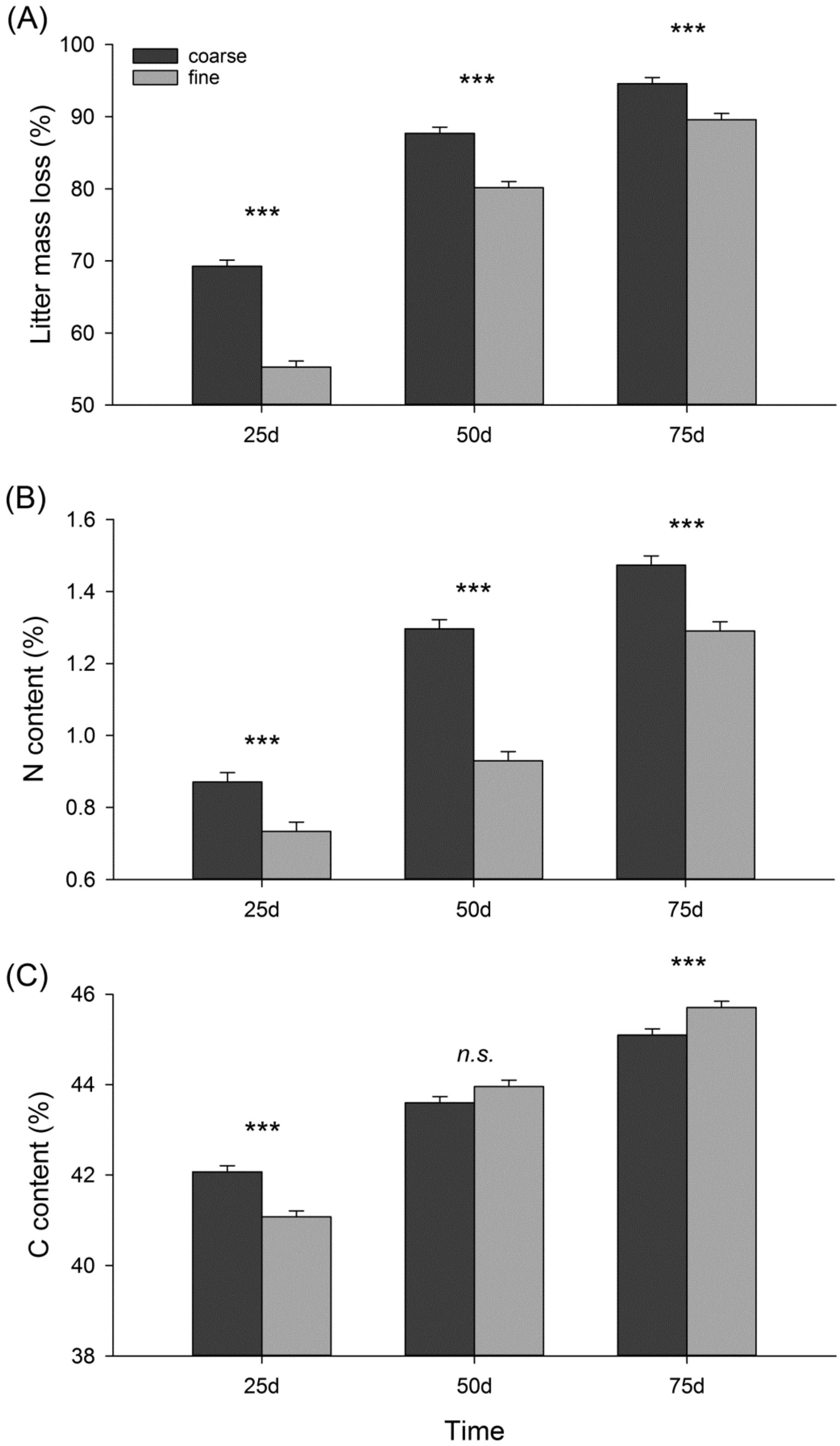
SUPPORTING INFORMATION



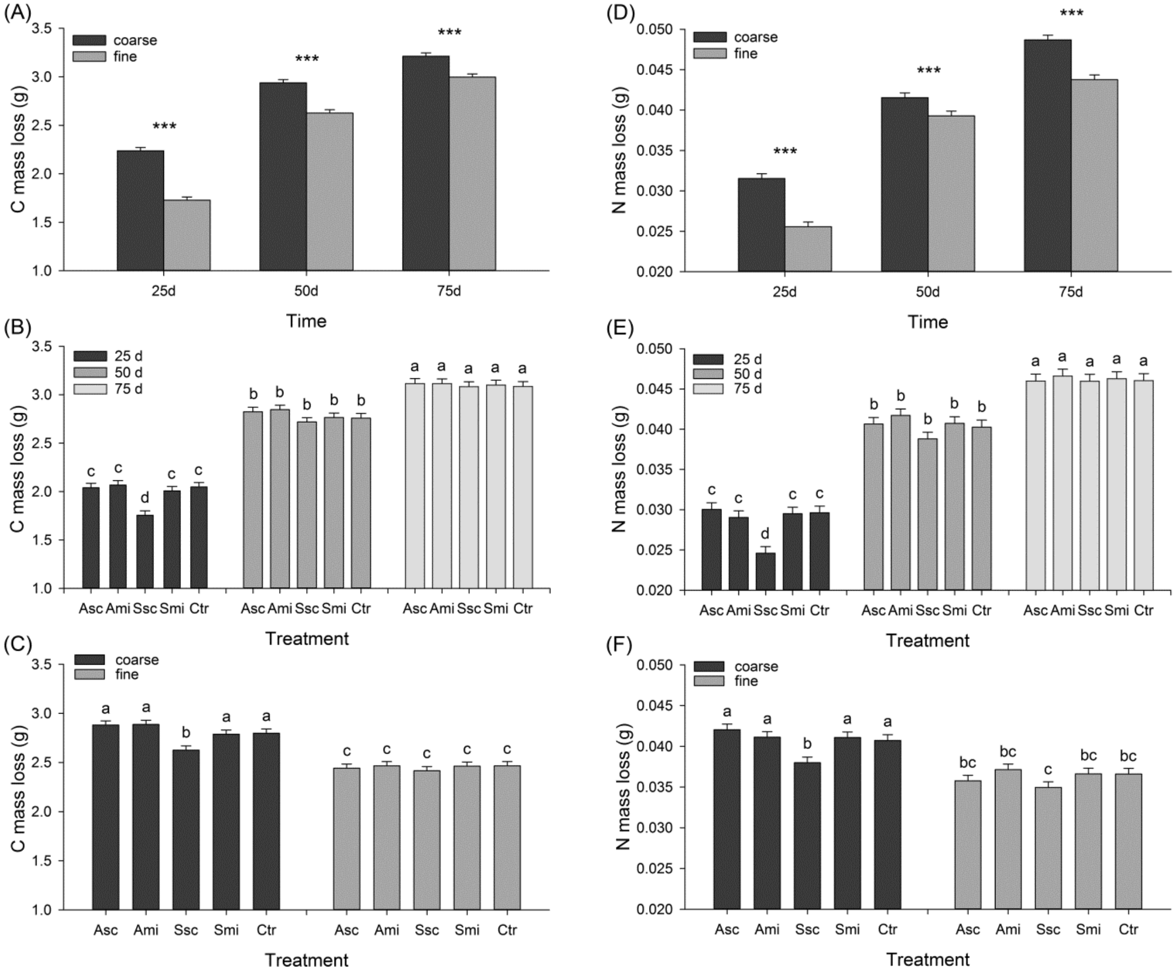
S1 Fig. C/N ratios: mesh size × time; treatment × time; mesh size × treatment. Comparison of C/N ratios (means + SE) of rice straw litter in (A) coarse- and fine-meshed litterbags at the three retrieval times, (B) bags under the five treatments at the three retrieval times, and (C) coarse- and fine-meshed bags under the five treatments. Different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). Asterisks in graph (A) indicate significant differences between the two mesh sizes at one point in time (not between times); $P \leq 0.001$***. Value of the original straw (= *time 0d*): C/N = 61.5. For abbreviations see Fig 1.



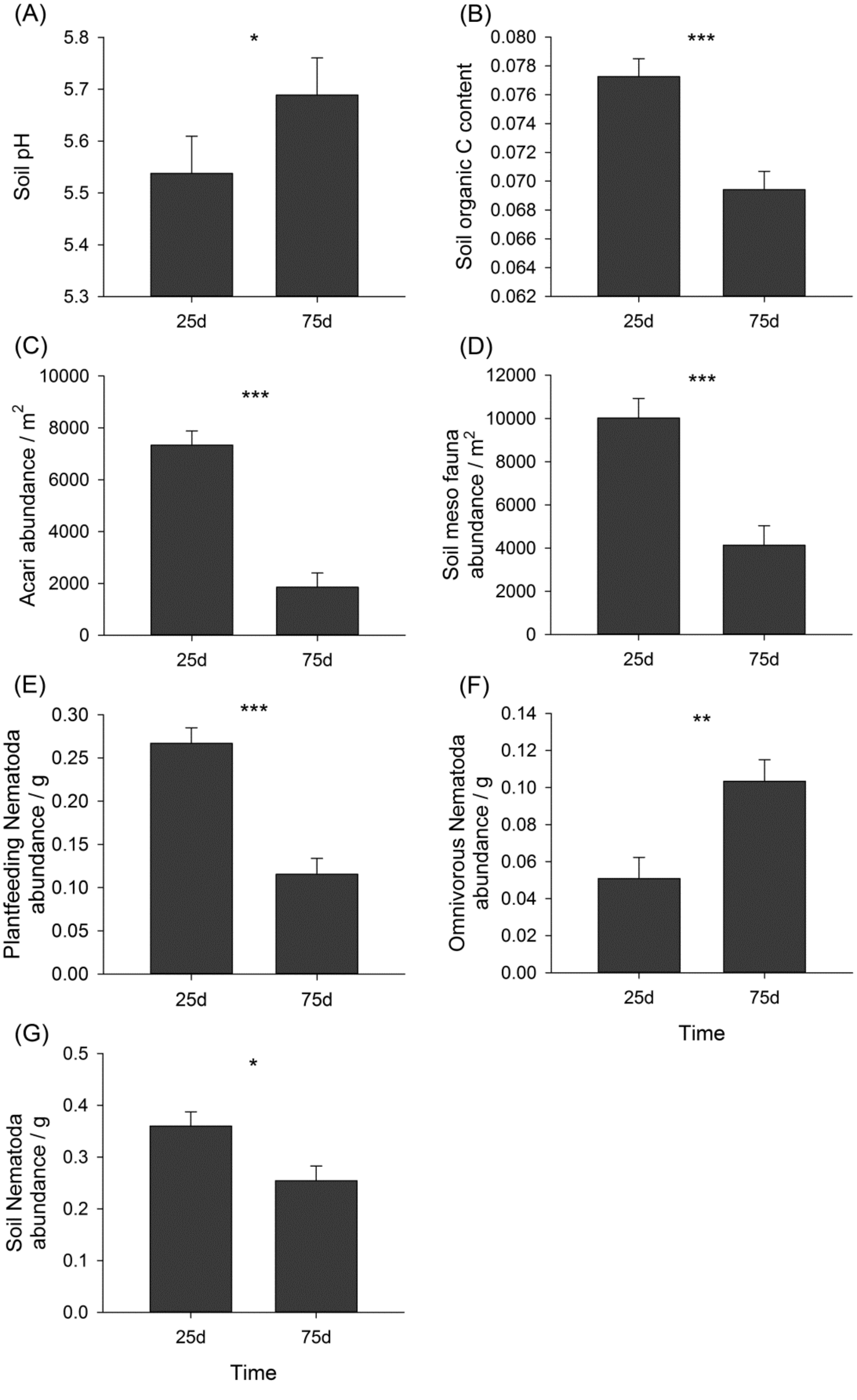
S2 Fig. Experimental setup. Experimental setup; treatment abbreviations: 'Asc' - ash of burned rice straw scattered on the field, 'Ami' - ash of burned rice straw mixed in the soil, 'Ssc' - rice straw scattered on the field, 'Smi' - rice straw mixed in the soil, 'Ctr' - control (no ash or straw added).



S3 Fig. Litter mass loss, N and C content: mesh size × time. Percent litter mass loss (A), N content (B) and C content (C) (means + SE) of rice straw litter in coarse- and fine-meshed bags retrieved at three points in time. Asterisks indicate significant differences between the two mesh sizes at one point in time (not between times); *P ≤ 0.001****. Values of the original straw (= *time 0d*): N = 0.6 %, C = 36.8 %.



S4 Fig. C & N mass loss: mesh size × time; treatment × time; mesh size × treatment. C-/ N mass loss (g) (means + SE) of rice straw litter in (A/D) coarse- and fine-meshed litterbags at the three retrieval times, (B/E) bags under the five treatments at the three retrieval times, and (C/F) coarse- and fine-meshed bags under the five treatments. Different letters above the bars indicate significant differences between means (Tukey's HSD, *$P \leq 0.05$*). Asterisks in graphs (A) and (D) indicate significant differences between the two mesh sizes at one point in time (not between times; *$P \leq 0.001$****). Values of the original straw (= *time 0d*): N = 0.06 g, C = 3.44 g. For abbreviations see Fig 1.



S5 Fig. Changes of soil traits and soil fauna abundances. Soil traits: pH (A) and organic C content (B); average numbers of selected soil fauna groups (C-G) per *'time'*; $P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***. Abundances of mesofauna (C & D) are given per m^2 soil area and abundances of soil nematodes (E-G) are given per g soil dry weight.

Table A in S1 File. The effects of ‘*treatment*’, ‘*time*’ , ‘*mesh*’ and their interactions on C/N ratios in the rice straw litter using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Factors	C/N ratio		
	Df	F	*P*
treatment	4,16	0.95	0.46
time	2,187	346	**< .0001**
mesh	1,206	215	**< .0001**
treatment × *time*	8,187	1.14	0.34
treatment × *mesh*	4,206	7.4	**< .0001**
mesh × *time*	2,206	20.8	**< .0001**
treatment × *mesh* × *time*	8,206	1.48	0.17

Factor ‘*treatment*’ represents the five different management practices (Asc, Ami, Ssc, Smi, Ctr; for abbreviations see Fig 1), the factor ‘*time*’ is the effect of the three different time periods for which the bags were left in the fields (25d, 50d, 75d), and factor ‘*mesh*’ the two mesh sizes (5 mm and 20 μm) used in every plot. The model also includes the random effects of the factors ‘*block*’ and ‘*replicate*’; these two factors and their interactions are not shown.

Table B in S1 File. The effects of '*treatment*', '*time*', '*mesh*' and their interactions on rice straw N and C mass loss using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Factors	N mass loss (g)			C mass loss (g)		
	Df	F	*P*	Df	F	*P*
treatment	4,16	6.42	**0.002**	4,16	4.18	**0.02**
time	2,187	836	**<.0001**	2,187	2146	**<.0001**
mesh	1,206	176	**<.0001**	1,206	679	**<.0001**
treatment × *time*	8,187	2.7	**0.01**	8,187	5.41	**<.0001**
treatment × *mesh*	4,206	2.61	**0.04**	4,206	9.71	**<.0001**
mesh × *time*	2,206	11.1	**<.0001**	2,206	43.3	**<.0001**
treatment × *mesh* × *time*	8,206	2.02	**0.04**	8,206	1.31	0.24

Factor '*treatment*' represents the five different management practices (Asc, Ami, Ssc, Smi, Ctr; for abbreviations see Fig 1), the factor '*time*' is the effect of the three different time periods for which the bags were left in the fields (25d, 50d, 75d), and factor '*mesh*' the two mesh sizes (5 mm and 20 μm) used in every plot. The model also includes the random effects of the factors '*block*' and '*replicate*'; these two factors and their interactions are not shown.

Table C in S1 File. The effects of *'treatment'*, *'time'* and their interaction on soil traits (pH, organic C content) and selected soil fauna groups using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Factors	Soil pH			Soil organic C content			Acari abundance / m^2		
	Df	F	*P*	Df	F	*P*	Df	F	*P*
treatment	4,16	0.61	0.66	4,16	0.49	0.74	4,16	1.52	0.24
time	1,18	4.53	**0.04**	1,18	34.1	**< .0001**	1,18	59.8	**<.0001**
treatment × *time*	4,18	1.1	0.39	4,18	0.9	0.49	4,18	2.18	0.11

	Soil meso fauna abundance / m^2			Plantfeeding Nematoda abundance / g			Omnivorous Nematoda abundance / g		
	Df	F	*P*	Df	F	*P*	Df	F	*P*
treatment	4,16	1.52	0.24	4,16	1.56	0.23	4,16	1.95	0.15
time	1,18	33.1	**<.0001**	1,18	40	**< .0001**	1,18	11.3	**0.003**
treatment × *time*	4,18	3.38	**0.03**	4,18	1.12	0.38	4,18	1.45	0.26

	Soil Nematoda abundance / g		
	Df	F	*P*
treatment	4,16	1.05	0.41
time	1,18	7.08	**0.02**
treatment × *time*	4,18	0.92	0.47

Factor *'treatment'* represents the five different management practices (Asc, Ami, Ssc, Smi, Ctr; for abbreviations see Fig 1) and the factor *'time'* is the effect of the two sampling dates of soil cores (25d, 75d). The model also includes the random effect of the factors *'block'*, which is not shown.

Table D in S1 File. Eigenvalues of the four RDA axes and their contribution to the total variance, as well as accumulated constrained ('Acc.') eigenvalues and contribution to the accumulated variation of the four RDA axes from the community analyses of aquatic and soil fauna abundances.

	RDA 1	RDA 2	RDA 3	RDA 4
Eigenvalue	4.08	1.88	1.09	0.86
Proportion explained (%)	11	5.08	2.93	2.34
Acc. eigenvalue	4.08	1.88	1.09	0.86
Acc. proportion explained (%)	51.6	23.8	13.7	10.9

Table E in S1 File. Centroids for factor constraints of the first two RDA axes. Highest absolute values are indicated in bold font.

	RDA 1	RDA 2
Ash mixed in	-0.91	0.35
Ash scattered	-0.60	0.61
Straw mixed in	0.51	**-2.11**
Straw scattered	**1.92**	0.99
Control	-0.92	0.16

Table F in S1 File. ANOVA table of permutation tests for the four RDA axes and the constraining environmental variable '*treatment*'; 'Perm' = number of permutations. Significant effects are indicated in bold font.

	Df	Var	Perm	F	*P*
RDA 1	1	4.08	199	2.81	**0.005**
RDA 2	1	1.88	199	1.29	0.15
RDA 3	1	1.09	99	0.75	0.81
RDA 4	1	0.86	99	0.59	0.93
Treatment	4	7.91	199	1.36	**0.02**

Chapter 4

COMPENSATORY MECHANISMS OF LITTER DECOMPOSITION UNDER ALTERNATING MOISTURE REGIMES IN TROPICAL RICE FIELDS

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ABSTRACT

A conversion from permanently flooded rice cropping systems into crop rotations including non-flooded upland crops gets increasingly popular in the tropics as it meets rising challenges for a sustainable food production in regard of water consumption and trace gas emissions. Shorter flooded periods and manipulation of fertilizer inputs affect belowground community composition, biomass and functioning. However, nothing is known about changes in soil biota and decomposition dynamics associated with these agricultural management shifts in rice fields. Our objective was to examine how crop diversification, different moisture regimes and nitrogen inputs influence decomposition dynamics and belowground invertebrate assemblages as well as their contribution to residue decomposition.

We conducted an experiment in Central Luzon Island, Philippines at lowland paddy fields with either continuously flooded, seasonally alternating wet and dry or continuously dry field conditions. Additionally, subplot treatments within these crop rotations included different N fertilizer management practices. We used litterbags with two different mesh sizes to assess decomposition with and without fauna over a period of 72 days. Soil microfauna and mesofauna were sampled at 36 plots in both seasons (dry and wet).

We hypothesized that: (I) during wet rice cropping decomposition rates associated with the microbial community will be limited due to anaerobic soil conditions increasing the impact of invertebrate decomposers on the decay of rice straw residuals, (II) the soil-dwelling invertebrate fauna will be modulated by changes in soil conditions, and (III) the emerging terrestrial groups of soil animals in non-flooded fields can compensate the ceasing contribution by (semi-)aquatic invertebrates to rice straw decomposition.

Although we found no link between faunal abundance and the contribution by invertebrates to rice straw decomposition, we could show that the actual water content in the soil is the decisive factor determining the activity of invertebrate decomposers as well as the composition and abundance of the soil fauna in fields with alternating cropping regimes. The impact of invertebrates on rice straw decomposition was significantly higher under anaerobic soil conditions which compensated the retarded microbial decay rates during wet rice cropping. In contrast, microbial decomposition rates were greatly accelerated under aerobic soil conditions whereas invertebrates had no significant influence on the mass loss of rice straw regardless of their higher abundance in dry fields. Thus, especially under flooded soil conditions, invertebrates were essential for an effective decay of rice straw residuals and can therefore be considered particularly important for a sufficient nutrient supply in inundated rice fields.

Keywords: Litterbag, detritivore, *Oryza sativa*, Philippines, soil fauna, crop rotation

Highlights:

- Significantly higher abundance of soil mesofauna under aerobic field conditions
- Invertebrates substantially contributed to straw decomposition in flooded fields
- No contribution by invertebrates to rice straw decomposition in non-flooded fields
- Highly accelerated microbial decomposition rates under aerobic soil conditions
- No link between faunal assemblages and invertebrate-driven rice straw decomposition

INTRODUCTION

Flooded rice cultivation with two or three crops per year is the most common agricultural land use type in the lowland tropics and subtropics of Asia (Cassman and Pingali 1995). These areas provide around 90 % of the global rice supply (FAO 2007, USDA 2007). Currently, sustainability of producing rice in flooded fields is questioned in respect to water use and emissions of greenhouse gases (Bouman et al. 2007, Mueller et al. 2012). Some management strategies have been developed to reduce the water consumption and methane emission from rice-based cropping systems while ensuring sufficient productivity (e.g. Wassmann and Vlek 2004). One of the most promising approaches is the inclusion of non-flooded upland crops into rice-dominated systems (Bouman et al. 2005, Timsina et al. 2010, Timsina et al. 2011). However, crop diversification in rice-based systems also bears risks as it possibly leads to a decrease of soil nutrients and to a decline in contents of soil organic matter (Witt et al. 2000, Haefele et al. 2013).

Paddy rice soils are habitats of dynamic assemblages of soil organisms (Bambaradeniya and Amarasinghe 2003) which significantly contribute to the processes of crop residue decomposition and element cycling (Lekha et al. 1989, Widyastuti 2002, Schmidt et al. 2015b). The belowground community of conventionally managed paddy soils is dominated by aquatic and semi-aquatic oligochaetes and nematodes while microarthropods are rather rare (Watanabe and Roger 1985). Changes in water management by introducing upland crops and changed amounts of fertilizer application constitute a high potential for disturbing the original assemblages of soil animals. A lower contribution by the soil fauna in decomposition processes can also decrease the microbial activity leading to reduced carbon (Setälä et al. 1988) and nitrogen (Huhta et al. 1988) mineralization. On the other hand, extended niche diversity in time due to crop diversification might increase the abundance and diversity of the belowground assemblages of animals along with their functional diversity (Cancela da Fonseca and Sarkar 1998) including litter decomposition. For example, soil mites and springtails have limited influence on the decomposition of organic matter in fields with continuously flooded rice cropping (Widyastuti 2002). However, under aerobic conditions their abundance rapidly increases (Widyastuti 2002) which in turn might enhance their functional importance, e.g., in regulating and controlling the microbial activity during decay processes.

Decomposition of soil organic matter is one of the most important and highly interactive functional processes regulating global nutrient cycling and energy flow in the soil (Lekha et al. 1989, Manzoni et al. 2008, Talbot and Treseder 2011). It involves a broad spectrum of micro-, meso- and macrofaunal groups (Wolters 1991, Anderson 1995, Coleman and Crossley 1996), which often have rather indirect effects in the decay process of organic matter, e.g. by increasing the surface area and the quality of the litter for microbial colonization (Heath et al. 1964). Hence, microbial activity and biomass is strongly modulated by higher trophic levels of a soil food web (Lekha et al. 1989, Singh et al. 2005). The rate of litter decomposition is also influenced by several biotic and abiotic factors, like soil properties (e.g. soil moisture and soil texture; Clark and Gilmour 1983, Merckx et al. 1985, Steinberger and Whitford 1988, Amato and Ladd 1992) and the biochemical composition of the plant residues (e.g. N availability and lignin concentrations; Bollen 1953, Tian et al. 1993, Singh et al. 2005, García-Palacios et al. 2013). Especially in wet rice fields, invertebrate decomposers are of paramount importance for effective litter decomposition, as high C/N ratios and lignin contents in the rice straw as well as the anaerobic conditions in flooded fields slow down microbial decomposition (Acharya 1935, Vigil and Kissel 1991, Koegel-Knabner et al. 2010, Schmidt et al. 2015b).

Witt et al. (2000) conducted a study on the impact of soil aeration and N fertilizer management (including crop residue incorporation) on the N cycling and C sequestration in continuous rice cropping and rice-maize rotation systems in which they provided evidence for the strong effects of different crop rotations on the organic C and N balance in the soil. Further, it has been shown that also the abundance and composition of soil faunal assemblages are particularly dependent on the kind of crop currently planted on the fields (Wardle et al. 1999). However, none of these studies considered the effects of changes in the composition of assemblages of soil animals due to a shift in soil conditions during varying crop rotations on the decomposition processes and the associated nutrient dynamics. Recently, Handa et al. (2014) reported for a variety of terrestrial and aquatic biomes that the reduction of the functional diversity of decomposer organisms slows down the cycling of litter derived C and N. Further, an increase in plant species richness after the introduction of alternating crop rotations can influence the biomass of microbes and soil animals (Wardle et al. 1999) which in turn might alter the speed of nutrient cycling in the soil. Consequently, improved knowledge about soil-dwelling decomposers and decomposition dynamics related to soil animals in rice-based agroecosystems is essential to evaluate the benefits and risks of introducing non-flooded crops in rice paddy soils, and hence, for developing effective management strategies.

In our experiment we examined how introducing non-flooded upland crops into the cropping cycles of continuously flooded rice cultivation with different fertilization regimes alter the assemblages of soil animals and the invertebrate-driven decomposition of rice straw. We addressed the following hypotheses:

(I) Compared to non-flooded fields microbial litter decomposition in flooded rice fields is decreased due to anaerobic soil conditions which increases the relative importance of invertebrate decomposers.

(II) A conversion of soil conditions from wet to dry within different crop rotations influences the composition of the invertebrate assemblages. We expect meso- and microarthropod groups to be more abundant under aerobic field conditions.

(III) The lack of aquatic invertebrates and their contribution to decomposition in soils of non-flooded fields is compensated by a more abundant and active terrestrial mesofauna.

MATERIAL AND METHODS

Study site

The study was conducted within the scope of two international projects, ICON (*“Introducing Non-Flooded Crops in Rice-Dominated Landscapes: Impact on Carbon, Nitrogen and Water Cycles”*) and LEGATO (*“Land-use intensity and Ecological Engineering - Assessment Tools for risks and Opportunities in irrigated rice based production systems”*; (Settele et al. 2015), at the ICON experimental fields of the International Rice Research Institute (IRRI) about 66 km south of Manila (Laguna, Philippines; elevation: approx. 20 m above sea level; coordinates: lat 14.2, lon 121.4 WGS84 decimal degrees). In this region lowland flooded rice is mostly cultivated in two crop cycles per year, one in the dry season (December - May) and one in the wet season (June - November). Our study was carried out during both seasons in 2013. Prior to the experiment, the site was used for paddy rice cultivation over decades.

Average minimum, mean and maximum temperature during the experiment (Dec. 2012 – Nov. 2013) was 24.0, 27.7 and 31.5 °C. The climate is characterized by an unequal distribution of precipitation over the year. The average rainfall per month during the dry season was 87.4 mm (Dec. 2012 – May 2013) and average monthly rainfall during the wet season (Jun. – Nov. 2013) was 343.0 mm (weather data provided by the Climate Unit of the International Rice Research Institute, Los Baños, Laguna, Philippines).

The soil of volcanic origin is clay-dominated, classified as "Andaqueptic Haplaquoll" (USDA classification) with 54.2 % clay, 32.8 % silt and 13 % sand. The bulk density of the topsoil (0-0.1 m) is 1.0 kg dm^{-3}, pH is 6.1 in average and the organic C content is about 1.8 %.

Study design

Fieldwork took place at 36 plots of the ICON field experiment (4 crop rotations × 3 fertilizer treatments × 3 replicates). The 12 ICON core fields (530 - 549 m² each, total area of about 150 m × 100 m) in two rows with six fields in each row (see Figure 1 for the core field design), representing an extended Before-After-Control-Impact (BACI) designed field experiment (Underwood 1994) arranged in a split-plot design without blocks. The fields were separated by field bunds and encompassed by grass verges (5 m in diameter). Since the dry season 2012 the fields were managed with four different crop rotations, with systematic triplication. One continuously flooded rotation represents the traditional double-rice cropping system with two plant growth seasons of lowland flooded rice per year (*Oryza sativa* L., NSIC Rc222, Tubigan 18; henceforth abbreviated by ‘R-WET’ [dry season: flooded rice – wet season: flooded rice]). In two different intermittently submerged rotations flooded rice during the wet season followed an upland crop during the dry season which was either aerobic rice (NSIC Rc192, Sahod Ulan 1; 'R-MIX' [dry season: aerobic rice – wet season: flooded rice]) or maize; (*Zea mays* L., Pioneer hybrid P3482YR; 'M-MIX' [dry season: maize – wet season: flooded rice]). The fourth treatment simulated a continuously aerobic crop rotation where maize was grown in the dry season and aerobic rice during the wet season ('M-DRY' [dry season: maize – wet season: aerobic rice]).

Each field was split into three plots with similar surface area (159 - 197 m^2) separated by field bunds with different N fertilization treatments randomized over two parallel rectangles of about 24 × 6 m and one square plot of approximately 12 × 12 m. One plot per field received no N fertilization at all (zero N), the second one was conventionally fertilized (conventional N, 130 kg N ha^{-1}) based on local farmers' practices, and the third treatment was a site-specific N fertilization method (site-spec. N), which represents a dynamically adjusted nutrient management strategy where fertilizer inputs are calculated with the IRRI 'Rice Crop Manager' (http://webapps.irri.org/ph/rcm/) for site-specific conditions (180 kg N ha^{-1}). Critical time points of fertilizer application were determined with the IRRI leaf color chart according to their chlorophyll content (LCC, Witt et al. 2005). N fertilizer was applied as urea three times per season. Additionally, muriate of potash and Solophos were applied at seasonal rates of 30 kg ha^{-1} K_2O and 30 kg ha^{-1} P_2O_5 for rice, and 30 kg ha^{-1} K_2O and 50 kg ha^{-1} P_2O_5 for maize, respectively.

Rice seedlings (flooded and aerobic rice) were raised in the greenhouse and transplanted into the fields 21 days after seeding (2 - 3 seedlings per hill with 0.2 × 0.2 m spacing). Flooded rice fields were kept submerged (approx. 0.05 m water body) after crop establishment (31 days after seeding) until two weeks before harvest. Land preparation consisted of soaking, plowing and puddling as well as harrowing and leveling. Maize and aerobic rice were grown in non-puddled soil. Fields were irrigated when rainfall was insufficient. Drainage ditches prevented fields with upland crops from flooding by heavy rain. Maize was planted with 0.25 m × 0.75 m seed spacing.

After harvest maize plants got completely removed from the fields (110 days after sowing) while rice plants were cut with approx. 5 cm high rice stubble residues remaining at the field (aerobic rice: 89 days after transplanting; flooded rice: 100 days after transplanting), which was incorporated into the soil during land preparation for the next plant growth season. Manual weeding and rodent control were performed once per season as well as molluscicide (organic "Kuhol buster" - saponin) and fungicide ("Score") application.

Litterbags

In order to quantify the contribution by invertebrate decomposers to total rates of decomposition, 10 g of litter (air-dried, chopped rice straw; *Oryza sativa* L., variety NSIC Rc222) were filled in nylon litterbags (15 × 20 cm) with two different mesh sizes (Bokhorst and Wardle 2013) and subsamples were retained for initial moisture and chemical analyses.

The fine-meshed litterbags had a mesh size of 20 µm × 20 µm and allowed access of microbes and part of the microfauna (e.g. fungi, bacteria, protozoa, micro-nematodes), while the coarse-meshed bags had a mesh size of 5 mm × 5 mm and allowed access of most of the invertebrate groups (Tian et al. 1992). Henceforth, we will refer to the litter mass losses in fine-meshed bags as 'microbial decomposition', since microarthropods, which possibly enter bags, where shown to have negligible influence on the decomposition process in flooded fields (Cancela da Fonseca and Sarkar 1998, Widyastuti 2002, Liang et al. 2005). Two weeks after transplanting or seeding one fine- and one coarse-meshed litterbag were embedded in the upper soil layer in the middle of each field (5-10 cm below the soil surface) with a minimum spacing of 20 cm between bags (total number of bags: 72 per season). Litterbags were retrieved after 72 days of exposure in the field (approx. two weeks before harvest). After retrieval of the bags, soil particles, roots, and other alien plant material adhering to the straw were removed. The cleaned straw was dried at 60 °C for at least three days and weighed to the nearest centigram to calculate litter mass losses. The C and N contents of the original straw as well as retrieved straw from each litterbag were determined using 'Elementar Vario EL element analyser' (Elementar Analysengeräte GmbH, Hanau, Germany).

Soil sampling

Soil biota was sampled from all 36 plots. The field sampling was carried out twice a season (total 144 sample sets). On each date, five soil core subsamples (approx. Ø 2 cm, 10 cm depth) were taken per plot for the extraction of nematodes following a modified Cobb's decanting and sieving method (Cobb 1918). The nematodes were identified to genus level and assigned to feeding groups (Yeates et al. 1993). For the mesofauna, two soil cores (approx. Ø 5 cm, 10 cm depth) were taken. Microarthropods were extracted using a MacFadyen high-gradient extractor (MacFadyen 1961) and were sorted, counted and identified to suborder or family level. The second soil core sample was manually sieved and decanted for the extraction of *Enchytraeidae* (potworms) which were suspended in 70 % ethanol and counted. Additional cores (Ø 5 cm, 10 cm depth) were used for the analyses of soil water content and total organic C content by the dry combustion method. As a proxy for fungal infestation, ergosterol, a fungal cell-membrane component, was measured according to Djajakirana et al. (1996). It was extracted from field-moist soil of 1 g dry weight with 100 ml distilled ethanol. The solution was shaken at 250 rev min^{-1} for 30 min. Ergosterol was further determined by reversed-phase HPLC with 100 % methanol as mobile phase and detected at a wavelength of 282 nm (Heinze et al. 2010).

Data analyses

We carried out split-split plot ANOVAs using general linear mixed models (GLMM) Type III sum of squares (procedure MIXED, SAS 9.2) to analyze litter-, C- and N mass loss as well as the relative contents of C and N in dependence on *crop* (crop rotation; 4 levels within main plot), *fert* (fertilization treatment; 3 levels within sub plot) and *mesh* (mesh size of litterbags; 2 levels within sub-sub plot) as well as their interactions. The factors *field(crop)* (main plot error) and *fert* × *field(crop)* (sub plot error) were considered random. Dry and wet season were analyzed separately to account for the fundamentally different abiotic conditions and to allow independent tests of the effect of the current status of flooding in the different crop rotations on the observed variables. C and N mass losses were calculated by including the straw dry weight and its relative C and N contents, respectively, before setting and after retrieving of litterbags. To describe the sole influence of invertebrate decomposers on litter mass losses (by excluding the proportion of microbial decomposition on litter mass loss in coarse-meshed bags) the log response ratio was calculated (LRR; ln of litter mass loss in course meshed bags divided by the litter mass loss in fine-meshed bags).

Using general linear mixed models (GLMM) Type III sum of squares (procedure MIXED, SAS 9.2), soil fauna data and ergosterol content were analyzed (split-split plot ANOVA) according to *crop* (crop rotation; 4 levels within main plot), *fert* (fertilization treatment; 3 levels within sub plot) and *time* (soil core sampling date; 4 levels within sub-sub plot for soil fauna / 2 levels within sub-sub plot for ergosterol) as well as their interactions. Again the terms *field(crop)* (main plot error) and *fert* × *field(crop)* (sub plot error) were considered random. Contrasts and post-hoc Tukey's HSD tests were carried out to reveal significant differences between the respective factor levels within factors.

To analyze community structures soil mesofaunal and nematode abundances were converted into individuals per m^2 and standardized using z-transformation. To reveal relations between assemblages of soil faunal abundances and the crop rotations (*crop;* categorical, 4 levels) within the two seasons (*time;* categorical, 4 levels) a redundancy analysis - RDA (Rao 1964, van den Wollenberg 1977) was carried out using R 2.1.4.2., package *vegan* (Oksanen et al. 2007). The variable *fert* (categorical, 3 levels) showed no significant influence on the community structure and was therefore removed from the model. We used this specific multivariate method, which requires linear relationships between faunal groups as well as between assemblages and environmental variables (Euclidean metric), because of the homogeneity in our dataset and the short environmental gradient (Leyer and Wesche 2007, Dormann and Kühn 2008). According to Lepš and Šmilauer (2003) the use of linear methods is appropriate, if the longest gradient calculated using DCA/DCCA is smaller than 3; in our dataset the longest gradient was 1.9.

Analyses of co-variance (ANCOVA) were used to analyze the relationships between litter mass losses and selected soil-dwelling faunal groups including the same fixed and random factors as in the above described ANOVAs on litter mass losses. Faunal groups were included successively as covariates to reveal linear relationships of variances. Structural equation models (SEM) are generally used to combine all independent and measured variables in a single model (Grace 2006). This method enabled us to test for direct and indirect interaction effects between our experimental and abiotic factors (crop rotation, fertilizer treatment and soil water content), faunal abundances (Oribatida, total abundance of Collembola, bacterial and fungal feeding nematodes), fungal biomass (ergosterol) and litter invertebrate-driven decomposition (log response ratio of litter mass loss; SPSS Amos 22.0.0). Seven observed endogenous variables were included in the model, one of them the soil water content as suspected important abiotic variable potentially determining soil faunal abundances as well as litter decomposition. The log response ratio (LRR) of litter mass loss was used as proxy for invertebrate decomposition rate. Two categorical exogenous predictor variables (crop rotation and fertilizer treatment) with four and three factor levels were “dummyfied” to include them in the model. For doing so a categorical variable with k distinct values needs to be converted into (k-1) dummy variables with binary coding [0, 1]. Therefore, *crop* was transformed into three variables (M-DRY, M-MIX, R-MIX) and *fert* into two variables (‘conv’ - conventional fertilization, ‘site’ - site specific fertilization). Dummy coding of categorical variables with more than two levels always works with comparing the respective variables with the remaining “un-coded” control variable. This means the effect of one dummy variable on an endogenous response variable is always in comparison to the one not included as dummy variable (R-WET for *crop* and ‘zero’ N for *fert*). For example, if a dummy variable has a negative regression weight of -0.4 on a response variable, the effect of the dummy variable is 40 % more negative than the effect of the control variable. As dummy variables are not independent from each other, they need to be co-varied. Model fitting was performed by the stepwise removal of unimportant relationships with confirmation of adequate model fits by a decrease of CAIC (Bozdogan 1987) by more than 2 (Grace 2006) and non-significant χ^2-tests ($P > 0.05$). However, in the wet season we observed only low abundances of the decomposer taxa and therefore excluded the SEM for this season.

RESULTS

Litter decomposition

The mass loss of rice straw in coarse- and fine-meshed litterbags was differently influenced by the four crop rotations (significant *crop* × *mesh* interactions, Table 1). In both seasons, flooded rice fields showed a much higher litter mass loss and N content in the straw retrieved from coarse-meshed bags compared to the ones with fine mesh (Figure 2, A-D). Independent of the respective crop rotation, fields during aerobic stages showed no significant differences between the two mesh sizes regarding litter mass loss and N content (Figure 2, A-D). However, compared to the original straw, which was filled into the litterbags, the retrieved straw generally showed increased relative N contents after decomposition (Figure 2 C+D; N content original straw = 0.6 %). Contrast tests of the *crop* × *mesh* interaction comparing the respective state of flooding in the particular season (flooded vs. non-flooded; $P < 0.05$) confirmed that the current state of flooding was more important in determining differences in litter mass loss and N contents in the retrieved straw (for both mesh sizes) than the crop rotations *per se*. C contents in the straw showed a reverse pattern with significant differences in non-flooded fields and no differences under flooded conditions (Figure 2, E+F). Changes in C content during decomposition showed no consistent pattern (Figure 2, E+F; C content original straw = 36.8 %). Total losses of C and N were smallest in fine-meshed bags retrieved from rice fields which were flooded in the particular seasons (S 1; S 2, A-D). The highest amounts of C and N were lost in straw retrieved from coarse-meshed litterbags of flooded fields as well as in straw which was retrieved from both mesh sizes in non-flooded fields. No significant differences in the range of these nutrient losses were evident (S 2, A-D). C/N ratios in litterbags with different mesh size and placed in different crop rotations reflect this pattern with lowest values in straw residues of coarse-meshed bags (in all fields) as well as fine-meshed bags during dry cropping. Highest values were found in fine-meshed bags during flooded cropping conditions (S 1; S 2, E+F). No significant effects of the factor *fert* (the three fertilizer treatments) or its interaction with *crop* and *mesh* on mass losses of rice straw, C and N as well as on C and N contents were verifiable (except for N content in the dry season, Table 1 and S 1).

Ergosterol contents in the soil as a proxy for fungal infestation showed a highly significant negative correlation with litter mass loss in fine-meshed bags ($r^2 = 0.25$; $P \leq 0.001$; Figure 3 - A); and further, a significant positive correlation with the log response ratio of litter mass loss ($r^2 = 0.29$; $P \leq 0.001$; Figure 3 - B; ANOVA table see S 3).

Invertebrate fauna

Acari and collembolans were the most abundant groups, with the highest abundances recorded in the dry season (Figure 4, A+B). The factors *crop* and *time* as well as their interaction significantly affected the abundances of all selected soil mesofaunal groups (except for *crop* on springtails; Table 2). Crop rotations significantly affected the abundances of Acari, but only in the end of the dry season, with the highest abundances recorded at M-DRY and the lowest at R-WET (Figure 4, A). Similarly, crop rotations affected the abundances of collembolans, but only in the beginning of the dry season, with the highest abundances recorded at M-MIX and the lowest at R-WET (Figure 4, B). Generally, very low abundances of soil mesofauna were recorded at R-WET as well as at all fields during the wet season (Figure 4, C). Fertilization significantly affected soil mesofauna only in interaction with time (Table 2).

In the RDA analysis the first RDA axis explained 8 % (S 4; $P = 0.005$) and represented mostly the ‘DS-end’ (end of dry season) level of the variable time (Figure 5; see also S 5 - highest absolute value at RDA 1). The second axis accounted for 4 % (S 4; $P = 0.005$) of the total variance and was related with the level ‘DS-start’ (start of dry season) of the variable time (Figure 5; see also S 5 - highest absolute value at RDA 2). In total, 14 % of the variance in the dataset was explained by the six constrained RDA axes. Of this variance 57 % was explained by RDA 1 and 26 % by RDA 2 (S 4). Both environmental factors, *crop* and *time*, had a significant influence on the abundance of different soil invertebrate groups (both $P = 0.005$; all results of ANOVA permutation tests are given in S 6). Analyses of co-variance revealed no significant relationships between litter mass loss in litterbags and abundance of different soil faunal groups.

During model fitting in SEM unimportant relationships were removed stepwise until the best fitting model was identified (model fit indices of fitted model: $\chi^2 = 11.0$, Df = 28, $P = 0.998$, CAIC = 134.75; for initial model see S 7); variables without any regression lines left during model fitting were removed from the model (‘Ergosterol’ and ‘Nematoda - fungal feeding’). The fitted SEM (Figure 6; for regression weights see S 8) revealed that 70 % of the variation in litter mass loss caused by invertebrates is explained by the net effects of its predictors. The highest influence on litter mass loss was mediated through soil water content (S 8 - highly significant positive regression weight of 0.72) which solely was determined by the three dummy variables describing the crop rotations (M-DRY, M-MIX, R-MIX; all three rotations with dry cropping during the dry season). Since all three path coefficients showed negative correlation values, R-WET most positively affects soil water content (for details on soil water contents within the seasons at the differently cultivated fields see S 9; ANOVA table see S 10). No direct or indirect effects of the surveyed faunal groups’ abundance on invertebrate-driven litter decomposition in the dry season were verifiable. The abundance of bacterial feeding nematodes was reduced by M-DRY treatment with a path coefficient of -0.45 while the abundance of Oribatida was supported by M-DRY (regression weight: 0.51). This reflects the results from the ANOVA analyses (Figure 4). Compared to zero N application, conventional and site specific fertilization treatments significantly increased the abundance of bacterial feeding nematodes with path coefficients of 0.35 and 0.41, respectively. With a regression weight of -0.44 soil water content had a direct negative effect on the total abundance of collembolans, while conventional fertilization of fields (compared to zero N application) increased their abundance significantly (regression weight: 0.32).

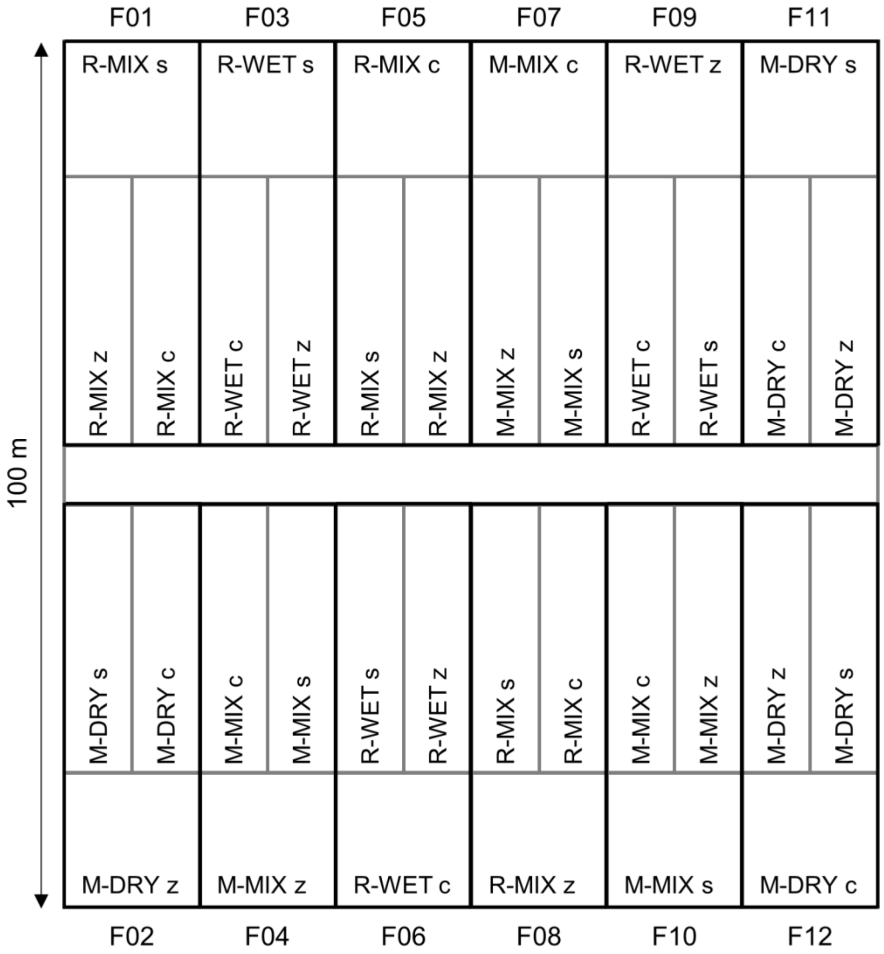

Figure 1 Setup of the ICON field experiment (scheme of the core field design). The 12 fields (530 - 549 m² each) are arranged in two rows. The fields are managed with four different crop rotations (R-WET: flooded rice in dry and wet season; R-MIX: aerobic rice in dry season – flooded rice in wet season; M-MIX: maize in dry season – flooded rice in wet season; M-DRY: maize in dry season – aerobic rice in wet season). Each field is split in two plots (159 - 197 m² each) with three different N fertilizer managements (z: no N fertilization; c: conventional N fertilizer application (130 kg N ha^{-1}); s: site-specific N fertilizer application (180 kg N ha^{-1})).

Table 1 The effects of *crop*, *fert* and *mesh* and their interactions on litter mass loss of rice straw and the N and C contents of the retrieved straw using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Dry Season	Litter mass loss (%)			N content (%)			C content (%)		
Factors	Df	F	*P*	Df	F	*P*	Df	F	*P*
crop	3,8	1.89	0.21	3,8	8.31	**0.01**	3,8	12.7	**0.002**
fert	2,16	0.25	0.78	2,16	4.67	**0.03**	2,16	0.16	0.86
mesh	1,24	9.54	**0.005**	1,24	5.60	**0.03**	1,24	38.8	**<.0001**
crop × *fert*	6,16	0.67	0.68	6,16	1.49	0.24	6,16	0.29	0.93
crop × *mesh*	3,24	13.5	**<.0001**	3,24	23.1	**<.0001**	3,24	10.3	**0.0001**
fert × *mesh*	2,24	0.46	0.64	2,24	0.36	0.7	2,24	2.45	0.11
crop × *fert* × *mesh*	6,24	0.14	0.99	6,24	1.80	0.14	6,24	0.90	0.51
Wet Season									
crop	3,8	2.96	0.1	3,8	4.64	**0.04**	3,8	0.80	0.53
fert	2,16	1.16	0.34	2,16	0.17	0.84	2,16	0.91	0.42
mesh	1,22	390	**<.0001**	1,22	213	**<.0001**	1,22	5.58	**0.03**
crop × *fert*	6,16	0.25	0.95	6,16	0.61	0.72	6,16	0.63	0.7
crop × *mesh*	3,22	28.1	**<.0001**	3,22	10.9	**0.0001**	3,22	7.20	**0.001**
fert × *mesh*	2,22	0.20	0.82	2,22	0.58	0.57	2,22	0.92	0.41
crop × *fert* × *mesh*	6,22	0.48	0.82	6,22	0.76	0.61	6,22	0.43	0.85

Factor *crop* represents the 4 different crop rotations (R-WET, R-MIX, M-MIX, M-DRY), the factor *fert* is the effect of the three different fertilizer treatments (zero, site specific, conventional), and factor *mesh* the two mesh sizes (5 mm and 20 µm) used in every plot. The model also includes the random effects of *field(crop)* (crop nested in field) and *fert* × *field(crop)*; their effects and interactions are not shown.

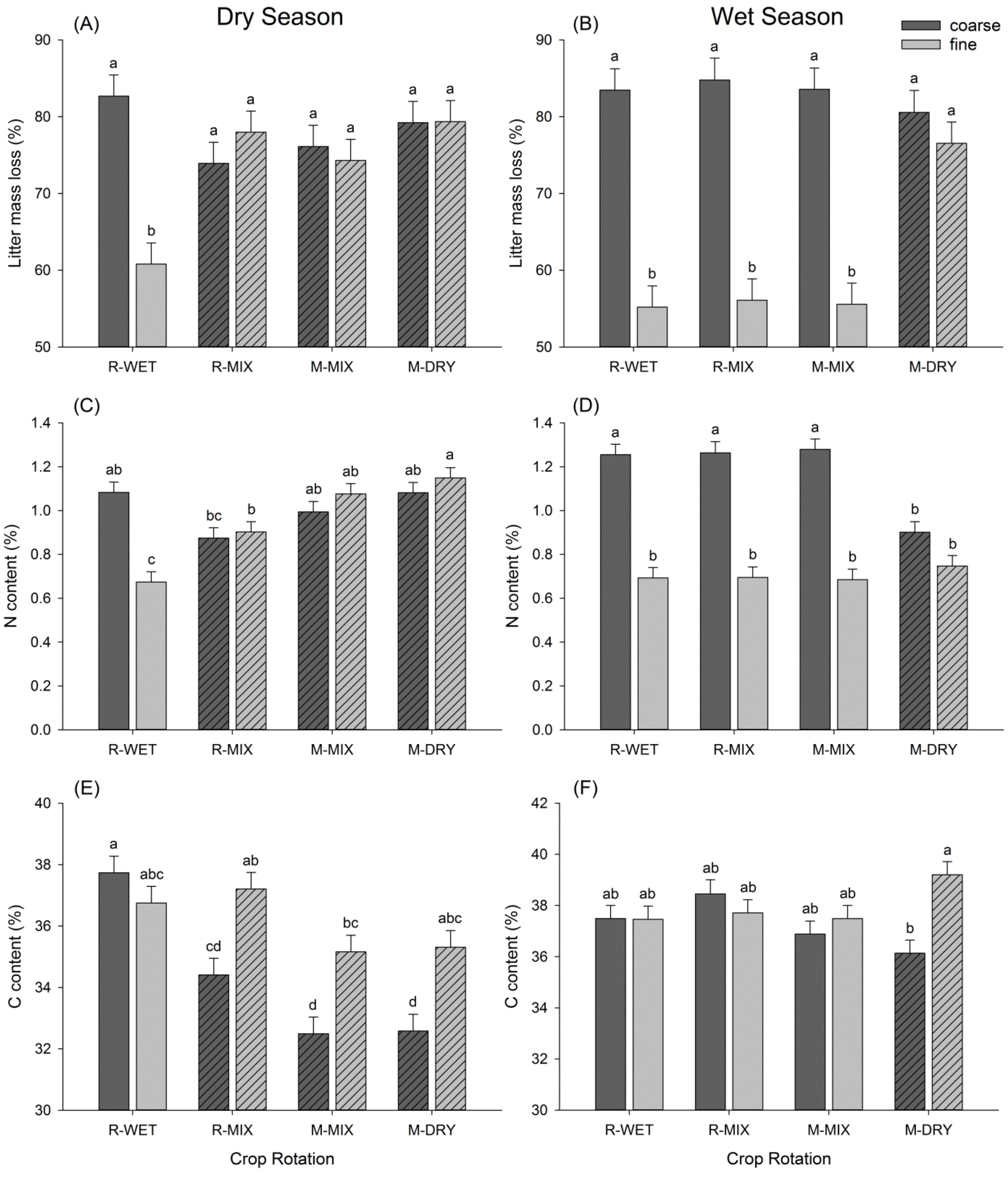

Figure 2 Percent litter mass loss (A/B), N content (C/D) and C content (E/F) (means + standard error SE) of rice straw retrieved from fields with different crop rotations in coarse-meshed (decomposition by invertebrates and microorganisms) and fine-meshed (decomposition by microorganisms) litterbags. A, C, E: dry season; B, D, F: wet season. Hatched bars constitute the aerobic variants in the particular season. Different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). Values of the original straw: N = 0.6 %, C = 36.8 %.

Table 2 The effects of *crop*, *fert* and *time* as well as their interactions on selected mesofaunal groups using a GLMM type III sum of squares. Significant effects are indicated in bold font.

	Acari / m^2			Collembola / m^2			Abundance of all meso-faunal groups / m^2		
Factors	Df	F	*P*	Df	F	*P*	Df	F	*P*
crop	3,8	8.44	**0.01**	3,8	2.43	0.14	3,8	9.26	**0.01**
fert	2,16	2.63	0.1	2,16	0.95	0.41	2,16	3.21	0.07
time	3,72	53.9	**<.0001**	3,72	16.1	**<.0001**	3,72	56.7	**<.0001**
crop × *fert*	6,16	0.97	0.48	6,16	2.71	**0.05**	6,16	1.48	0.25
crop × *time*	9,72	5.56	**<.0001**	9,72	3.45	**0.001**	9,72	4.29	**0.0002**
fert × *time*	6,72	2.25	**0.04**	6,72	2.40	**0.04**	6,72	2.84	**0.02**
crop × *fert* × *time*	18,72	0.58	0.9	18,72	1.52	0.11	18,72	0.65	0.85

Factor *crop* represents the 4 different crop rotations (R-WET, R-MIX, M-MIX, M-DRY), the factor *fert* is the effect of the three different fertilizer treatments (zero, site specific, conventional), and factor *time* the effect of the four different points in time the mesofauna was collected (DS-start, DS-end, WS-start, WS-end). The model also includes the random effects of *field(crop)* (crop nested in field) and *fert* × *field(crop)*; their effects and interactions are not shown.

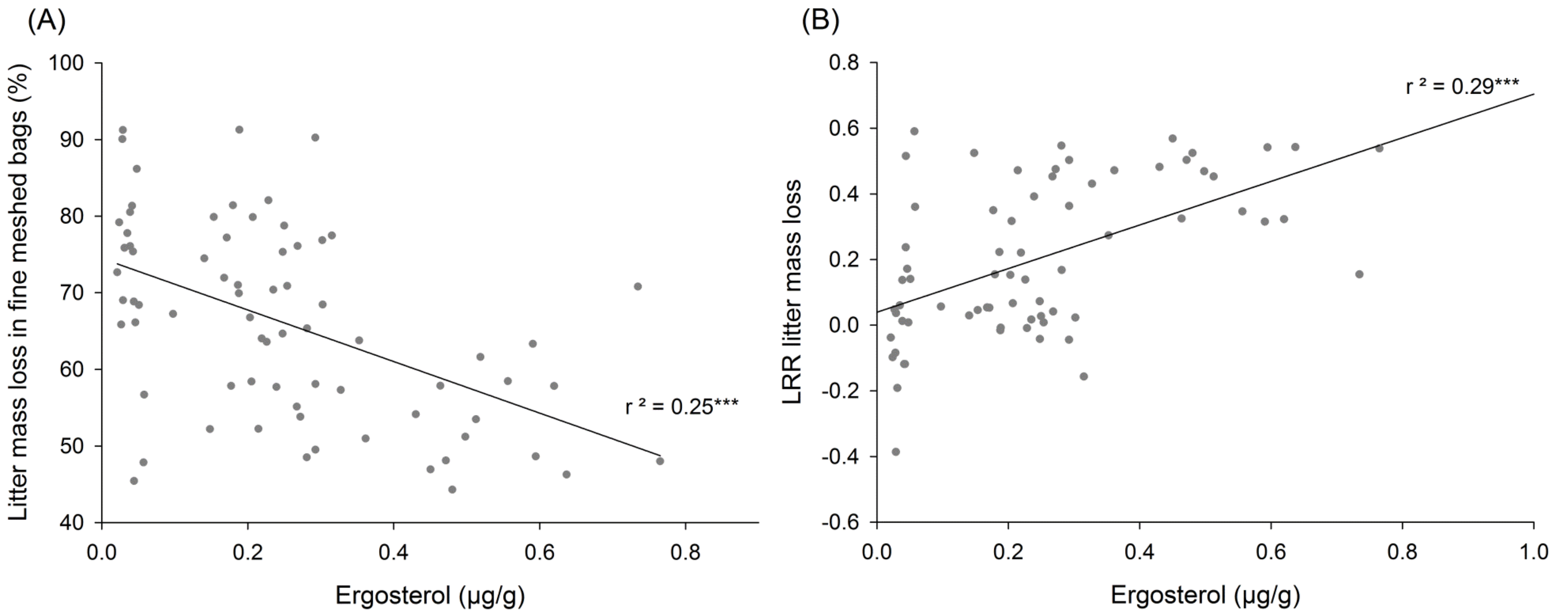

Figure 3 Linear regressions between (A) microbial contribution to litter mass loss (fine-meshed bags) with the ergosterol content in the soil (µg per g soil dry mass); and (B) the log response ratio of litter mass loss and ergosterol content in the soil (data of both seasons); $P \leq 0.001$***.

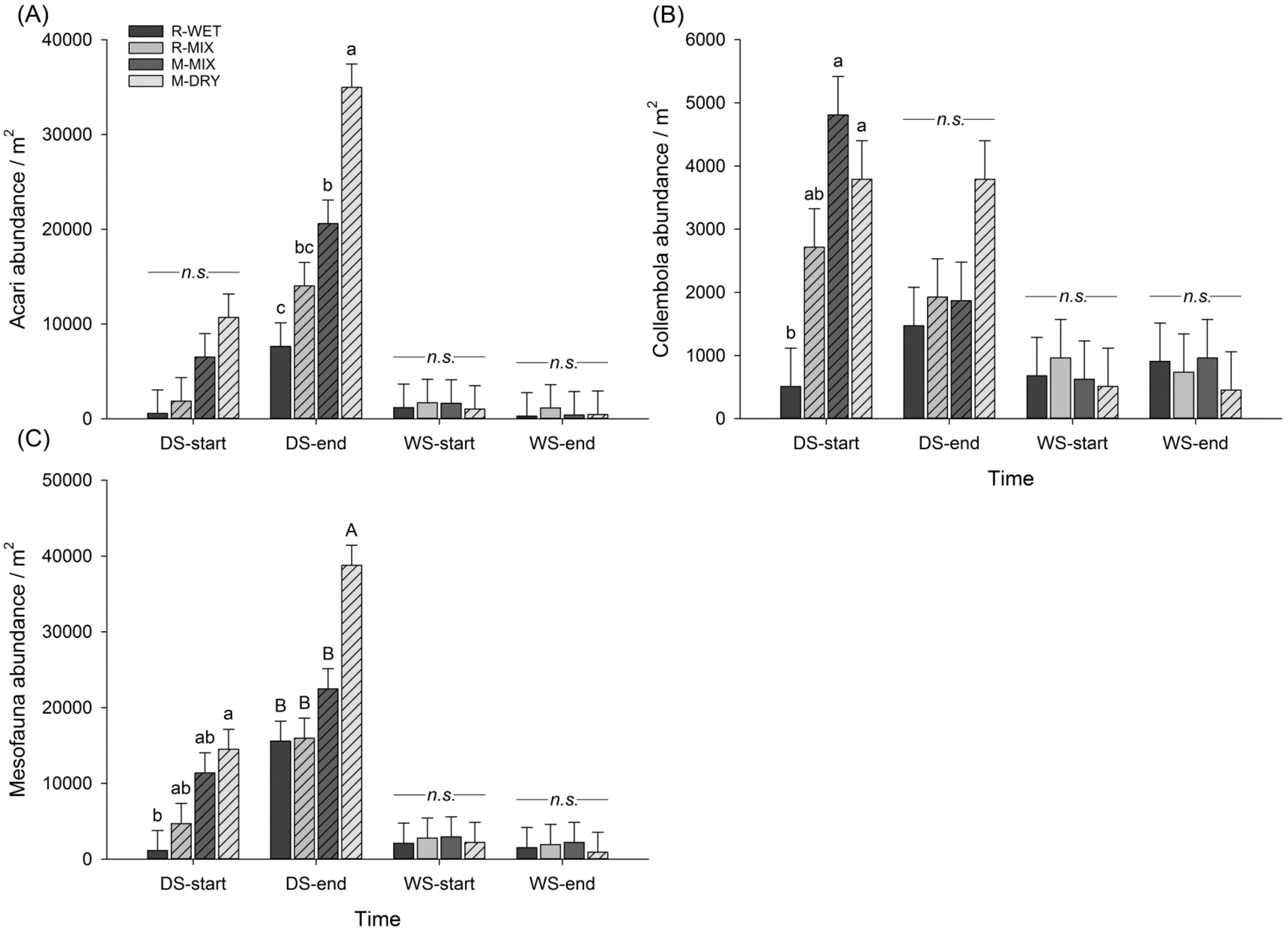

Figure 4 Abundance of soil mites (A) and springtails (B) per *crop* at the four sampling times (number of individuals). Panel (C) shows the total number of all mesofaunal groups (means + SE). Hatched bars constitute the aerobic variants in the particular season. Different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). Post-hoc comparisons were only made within one point in time, not between times.

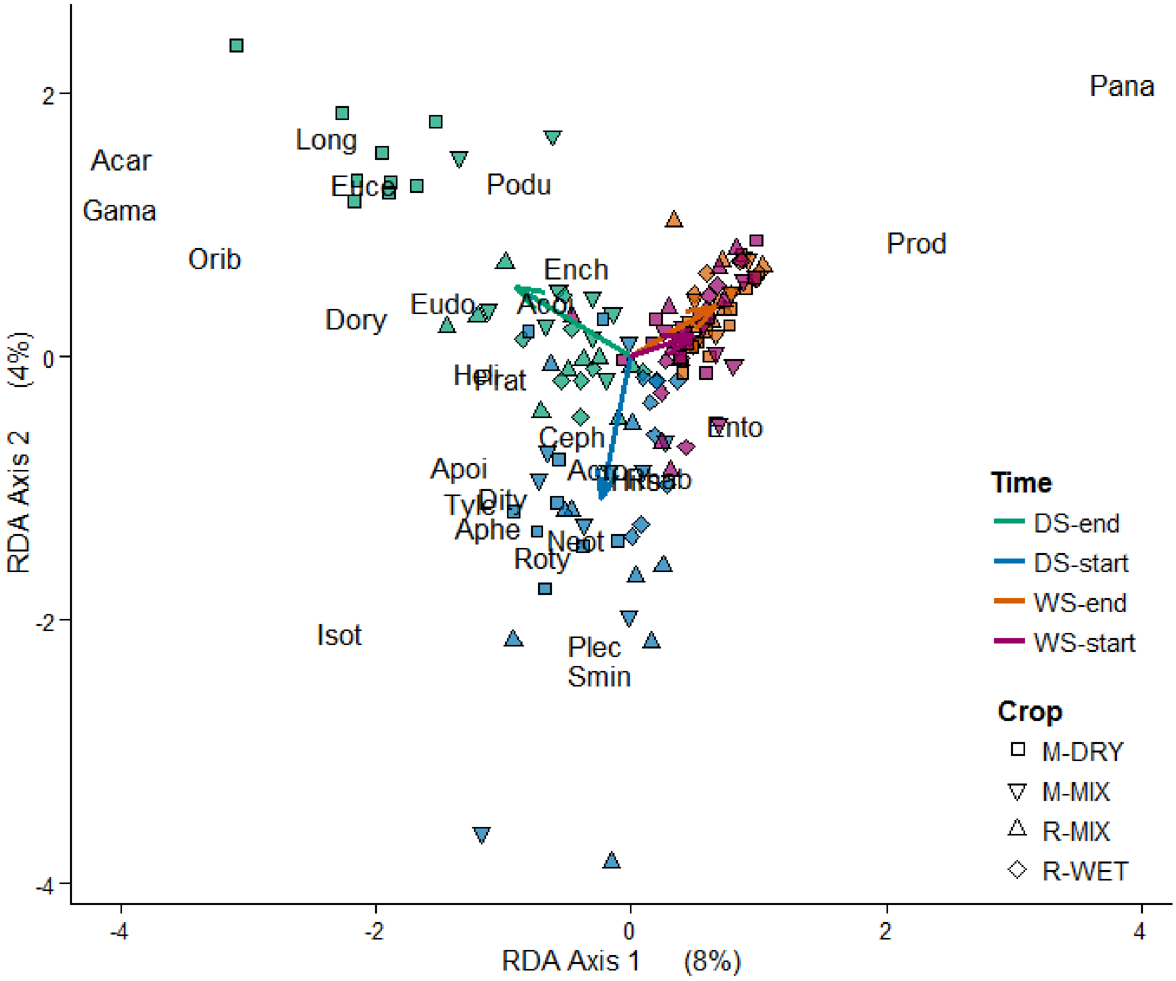

Figure 5 Euclidean distance biplot based on a redundancy analysis (RDA); faunal groups of soil samples are represented by their 4-letter-abbreviations (see below). Site scores are shown with different shapes depending on their affiliation to the particular crop rotation (*crop*), and different colors illustrate the corresponding point in time of each season (*time*). Treatment arrows represent the factor *time*. Axis 1 explains proportionally 8 % ($P \leq 0.01$) of the variation in the dataset; Axis 2 accounts for 4 % ($P \leq 0.01$) of the variation.

Abbreviations of faunal groups: Ench - Enchytraeidae; *Acari:* Orib - Oribatida, Gama - Gamasina, Acar - remaining Acari from soil samples (others than Orib and Gama); *Collembola:* Smin - Sminthuridae, Isot - Isotomidae, Podu - Poduromorpha, Ento - Entomobryomorpha; *Bacterial feeding nematodes:* Acro - Acrobeles spp., Acoi - Acrobeloides spp., Ceph - Cephalobus spp., Euce - Eucephalobus spp., Pana - Panagrolaimus spp., Plec - Plectus spp., Rhab - Rhabditis spp.; *Fungal feeding nematodes:* Apoi - Aphelenchoides spp., Aphe - Aphelenchus spp., Neot - Neotylenchus spp.; *Omnivorous nematodes:* Dory - Dorylaimus spp., Eudo - Eudorylaimus spp., Prod - Prodorylaimus spp.; *Plant feeding nematodes:* Dity - Ditylenchus spp., Heli - Helicotylenchus spp., Hirs - Hirshmanniella spp., Long - Longidorus spp., Prat - Pratylenchus spp., Roty - Rotylenchus spp., Tyle - Tylenchus spp.

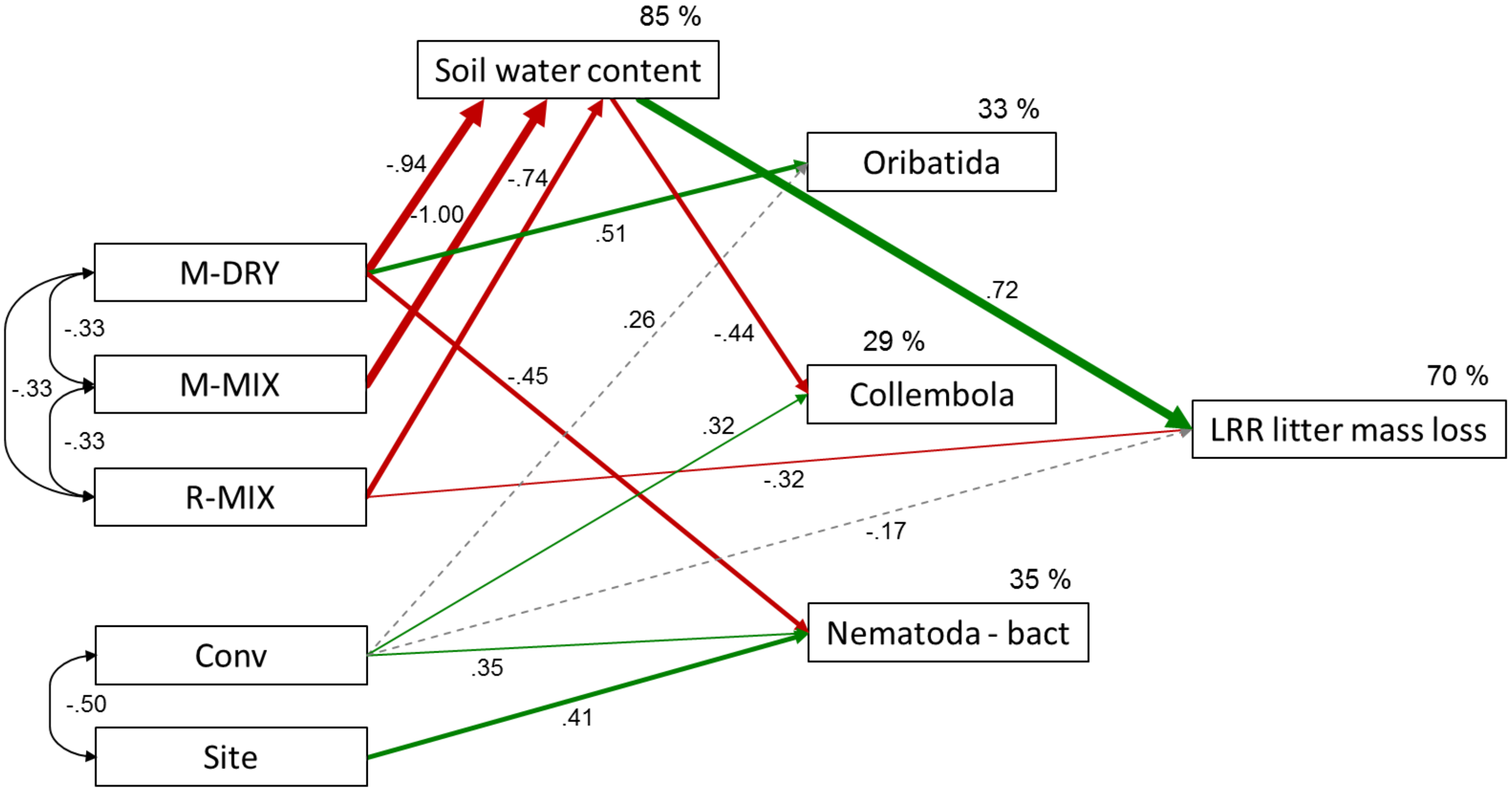

Figure 6 SEM - fitted model (dry season); model fit indices: $\chi^2 = 11$, Df = 28, *P = 0.99*, CAIC = 134.75; numbers above factors and regression lines represent standardized estimates of explained variance and regression weights; higher regression weights are indicated by thicker lines, for details on regression weights see S **8**; red lines represent negative path coefficients, green lines represent positive paths, dashed lines represent non-significant paths; "Nematoda - bact" = bacterial feeding nematodes; "Collembola" = total abundance of all groups of collembolans; "Conv" = conventional fertilization treatment; "Site" = site specific fertilization treatment; "LRR litter mass loss" = log response ratio of litter mass loss.

DISCUSSION

The role of invertebrates in the decay of crop residues in tropical paddy fields is still a rarely addressed topic (Settle et al. 1996, Schmidt et al. 2015a). Several studies in a variety of agroecosystems demonstrated the importance of invertebrates in the process of litter decomposition (e.g. Schädler and Brandl 2005, Wall et al. 2008, Gießelmann et al. 2010). However, those results are not easily transferable to our study system, as flooded rice cultivation creates a unique ecological habitat harboring quite peculiar assemblages of decomposers in the water as well as in the soil (Bambaradeniya and Amarasinghe 2003). Nevertheless, our results confirmed our expectation that invertebrate decomposers are key organisms promoting an effective decay of organic matter in rice-based agroecosystems.

Invertebrate decomposers are assumed to be of particular importance for the decay of crop residues in flooded paddy soils (Santos and Whitford 1981, Reddy et al. 1994, Widyastuti 2002) as the low availability of oxygen leads to a decrease of microbial mineralization processes (Acharya 1935). Further, microbial decay rates are highly influenced by the availability of C and N in the litter and in the soil (Jansson 1958, Knapp et al. 1983, Tian et al. 1995). The high C/N ratios of rice straw residuals (approx. 61, see S 2), compared to other herbaceous plant species (e.g. ranging from 19 to 30; see Schädler et al. 2003), make them hardly decomposable for microorganisms. This is reflected by our results as coarse-meshed bags retrieved from flooded fields always showed significantly higher litter mass losses compared to fine-meshed ones. Generally, invertebrate decomposers have rather indirect effects on the decomposition of crop residues. For example, pre-digesting parts of the litter can enhance the palatability for microbes. Further, by breaking down the plant material into smaller pieces and mixing them with the soil they can increase the residue-soil contact creating a more stable and favorable environment for microbial decomposers (Cogle et al. 1987, Singh et al. 2010).

In our experiment, invertebrates contributed to rice straw decomposition under flooded soil conditions as demonstrated by the higher losses of litter biomass from coarse-meshed litterbags compared to fine-meshed ones. This pattern corroborates the results of several previous field studies (Widyastuti 2002, e.g. Schmidt et al. 2015a, Schmidt et al. 2015b) and supports our first hypothesis that invertebrates contribute to the mass loss of rice straw in paddy fields. Similar changes of C contents in the rice straw retrieved from both types of litterbags indicate a primarily microbial-driven C-breakdown under flooded soil conditions. This might be due to the high C demand of the microbial community under anaerobic conditions (Lønborg and Søndergaard 2009) together with the N-limitation of microbial growth and decay rates. Overall, under anaerobic conditions the relative C and N contents in the rice straw increased during the time of our experiment (higher values after retrieval compared to initial ones). This might be due to the high leaching of other soluble components, like silicon or potassium (Christensen 1985, Saha et al. 2009). The rice straw used in our study contained particularly high amounts of silicon (Klotzbücher et al. 2015) which gets reduced quite fast in flooded fields (Ma and Takahashi 1989) resulting in higher losses of silicon during decomposition compared to C and N. The process of microbial decay includes bacteria and fungi (Tengerdy and Szakacs 2003). As we found no differences in litter mass losses in bags placed in dry fields during both seasons, microbial decomposition rates were relatively constant during the whole year. However, fungal biomass (ergosterol content µg g^{-1}) was notably higher in the wet season. Hence, in our experiment microbial decomposition during dry cropping might have been primarily induced by bacteria rather than fungi. In contrast, the increased fungal biomass in flooded paddy fields together with the significantly lower microbiota-induced mass loss of rice straw indicate a reduced bacterial activity with fungi as the main actors in microbial decomposition processes under flooded anaerobic conditions (Baldy et al. 2007, Bergfur and Friberg 2012). Fungal colonization of plant material increases its nutritional value (Graca 2001, Martinez et al. 2014, Perez et al. 2014) creating more attractive conditions for detritivores (Bradford et al. 2002). Hence, we found a positive correlation between ergosterol content and invertebrate-driven rice straw decomposition (log response ratio of litter mass loss).

Invertebrate decomposers in inundated rice fields mostly comprise (semi-)aquatic and edaphic groups including chironomid larvae, enchytraeids, microcrustaceans and nematodes (Weerakoon and Samarasinghe 1957, Kurihara 1989, Simpson et al. 1993b, a, Bambaradeniya and Amarasinghe 2003). Further, terrestrial agricultural soils harbor a tremendous diversity of microbial communities and faunal groups (Wardle et al. 2004) including nematodes, springtails, soil mites and enchytraeids (Giller 1996, Sileshi and Mafongoya 2006, da Silva Moço et al. 2009). The faunal assemblages in soils, used for flooded rice production is adapted to periodical changes in water availability between cropping and fallow phases (Bambaradeniya and Amarasinghe 2003) and needs to recover after the relatively short times without flooding (fallow phases). The establishment of crop rotations with alternating flooded and non-flooded crops greatly prolonged the dry periods. However, contrary to our expectations, the longer time of the dry phases has not negatively influenced the decomposition activity of invertebrates in the next wet phase. This explains the finding that faunal contribution to litter mass loss was consistently highest in flooded paddy fields.

In our experiment, mesofaunal abundance was generally higher during dry upland cropping compared to flooded paddy fields. Hence, in fields with continuously flooded rotations (R-WET) faunal groups were low in abundance throughout the year. We had expected significantly higher abundances of terrestrial invertebrates in fields with continuously dry cropping (M-DRY). However, in these fields we recorded the same shifts of faunal assemblages and abundance between dry and wet season as in fields with rotating moisture regimes (M-MIX, R-MIX). Presumably, this can be attributed to high soil moisture contents during the wet season independent on irrigation or drainage. Hence, soil water content seems to be the major determinant for these assemblages rather than the crop rotations *per se*. This conclusion is supported by our analyses on the composition of the assemblages of soil animals as the time of data acquisition (wet or dry season) was the most important variable for explaining the highest amount of variation in the dataset. Further, we could show that in the dry season abundances of selected decomposer groups (mites and collembolans) were directly or indirectly promoted by lower soil water contents. We expected these terrestrial animal groups compensate the decrease of rice straw decomposition by (semi-)aquatic invertebrates during dry cropping. However, although significantly higher abundances of mesofaunal groups were recorded in aerobic fields, their contribution to litter mass loss was negligible.

In contrast to our third hypothesis, in neither of the two seasons we found any relationship between faunal assemblages and invertebrate-driven decomposition rates. In the wet season invertebrates significantly enhanced the loss of rice straw in our litterbags, but their abundances were rather low. By contrast, in the dry season we found greatly increased numbers of invertebrates, but they had no influence on the decomposition of rice straw residuals. However, during this time the highly enhanced microbial biomass and decomposition activity completely compensated for the lack of contribution by invertebrate decomposers in our coarse-meshed litterbags. Hence, total litter mass losses did not differ between the two seasons, even though mesofaunal abundances did.

CONCLUSION

Our study demonstrates that the conversion from continuously flooded rice cultivation to an alternating cropping regime including dry upland crops affects the soil-dwelling fauna along with their contribution to decomposition processes. Under flooded soil conditions the invertebrate-driven decomposition of rice straw completely compensates for the low microbial decay rates. *Vice versa*, during dry cultivation phases microbial decomposition rates are significantly accelerated while the invertebrate contribution is negligible despite an increase of animal abundances. This indicates a complementarity of decomposition pathways in different cropping regimes. We may conclude that the introduction of non-flooded upland crops into the rice cycle is a promising approach with a number of ecological and economic advantages and with negligible consequences for decomposition as a fundamental ecosystem function.

ACKNOWLEDGEMENTS

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REFERENCES OF CHAPTER 4

Acharya, C. N. 1935. Studies on the anaerobic decomposition of plant materials: III. Comparison of the course of decomposition of rice straw under anaerobic, aerobic and partially aerobic conditions. Biochemical Journal **29**:1116-1120.

Amato, M., and J. N. Ladd. 1992. Decomposition of 14C-labelled glucose and legume material in soils: Properties influencing the accumulation of organic residue C and microbial biomass C. Soil Biology and Biochemistry **24**:455-464.

Anderson, J. M. 1995. Soil Organisms as Engineers: Microsite Modulation of Macroscale Processes. Pages 94-106 *in* C. G. Jones and J. H. Lawton, editors. Linking Species & Ecosystems. Springer US.

Baldy, V., V. Gobert, F. Guerold, E. Chauvet, D. Lambrigot, and J. Y. Charcosset. 2007. Leaf litter breakdown budgets in streams of various trophic status: effects of dissolved inorganic nutrients on microorganisms and invertebrates. Freshwater Biology **52**:1322-1335.

Bambaradeniya, C. N. B., and F. P. Amarasinghe. 2003. Biodiversity associated with the rice field agroecosystem in Asian countries: A brief review. Working Paper 63, Colombo, Sri Lanka: International Water Management Institute.

Bergfur, J., and N. Friberg. 2012. Trade-offs between fungal and bacterial respiration along gradients in temperature, nutrients and substrata: Experiments with stream derived microbial communities. Fungal Ecology **5**:46-52.

Bokhorst, S., and D. A. Wardle. 2013. Microclimate within litter bags of different mesh size: Implications for the ‘arthropod effect’ on litter decomposition. Soil Biology and Biochemistry **58**:147-152.

Bollen, W. B. 1953. Mulches and soil conditioners: carbon and nitrogen in farm and forest products. Agric. Food Chain. **1**:379-381.

Bouman, B. A. M., E. Humphreys, T. P. Tuong, and R. Barker. 2007. Rice and Water. Pages 187-237 *in* L. S. Donald, editor. Advances in Agronomy. Academic Press.

Bouman, B. A. M., S. Peng, A. R. Castañeda, and R. M. Visperas. 2005. Yield and water use of irrigated tropical aerobic rice systems. Agricultural Water Management **74**:87-105.

Bozdogan, H. 1987. Model selection and Akaike's Information Criterion (AIC): The general theory and its analytical extensions. Psychometrika **52**:345-370.

Bradford, M. A., G. M. Tordoff, T. Eggers, T. H. Jones, and J. E. Newington. 2002. Microbiota, fauna, and mesh size interactions in litter decomposition. Oikos **99**:317-323.

Cancela da Fonseca, J. P., and S. Sarkar. 1998. Soil microarthropods in two different managed ecological systems (Tripura, India). Applied Soil Ecology **9**:105-107.

Cassman, K. G., and P. L. Pingali. 1995. Intensification of irrigated rice systems: Learning from the past to meet future challenges. GeoJournal **35**:299-305.

Christensen, B. T. 1985. Wheat and barley straw decomposition under field conditions: Effect of soil type and plant cover on weight loss, nitrogen and potassium content. Soil Biology and Biochemistry **17**:691-697.

Clark, M. D., and J. T. Gilmour. 1983. The Effect of Temperature on Decomposition at Optimum and Saturated Soil Water Contents. Soil Science Society of America Journal **47**:927-929.

Cobb, N. A. 1918. Estimating the Nema Population of Soil. Bureau of Plant Industry, U.S. Department of Agriculture, Washington DC, USA.

Cogle, A. L., W. M. Strong, P. G. Saffigna, J. N. Ladd, and M. Amato. 1987. Wheat straw decomposition in subtropical Australia. II. Effect of straw placement on decomposition and recovery of added ^{15}N-urea. Australian Journal of Soil Research **25**:481-490.

Coleman, D. C., and D. A. Crossley. 1996. Fundamentals of soil ecology. Academic Press, New York, USA.

da Silva Moço, M. K., E. F. da Gama-Rodrigues, A. C. da Gama-Rodrigues, R. C. R. Machado, and V. C. Baligar. 2009. Soil and litter fauna of cacao agroforestry systems in Bahia, Brazil. Agroforestry Systems **76**:127-138.

Djajakirana, G., R. G. Joergensen, and B. Meyer. 1996. Ergosterol and microbial biomass relationship in soil. Biology and fertility of soils **22**:299-304.

Dormann, C. F., and I. Kühn. 2008. Angewandte Statistik für die biologischen Wissenschaften. Helmholtz Zentrum für Umweltforschung-UFZ **2**.

FAO. 2007. Food and Agriculture Organization of the United Nations. www.fao.org.

García-Palacios, P., F. T. Maestre, J. Kattge, and D. H. Wall. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecology Letters **16**:1045-1053.

Gießelmann, U. C., K. G. Martins, M. Brändle, M. Schädler, R. Marques, and R. Brandl. 2010. Diversity and ecosystem functioning: Litter decomposition dynamics in the Atlantic Rainforest. Applied Soil Ecology **46**:283-290.

Giller, P. S. 1996. The diversity of soil communities, the ‘poor man's tropical rainforest’. Biodiversity & Conservation **5**:135-168.

Graca, M. A. S. 2001. The role of invertebrates on leaf litter decomposition in streams-a review. International Review of Hydrobiology **86**:383-393.

Grace, J. B. 2006. Structural Equation Modeling and Natural Systems. Cambridge University Press, New York.

Haefele, S. M., N. P. M. Banayo, S. T. Amarante, J. D. L. C. Siopongco, and R. L. Mabesa. 2013. Characteristics and management options for rice–maize systems in the Philippines. Field Crops Research **144**:52-61.

Handa, I. T., R. Aerts, F. Berendse, M. P. Berg, A. Bruder, O. Butenschoen, E. Chauvet, M. O. Gessner, J. Jabiol, M. Makkonen, B. G. McKie, B. Malmqvist, E. T. H. M. Peeters, S. Scheu, B. Schmid, J. van Ruijven, V. C. A. Vos, and S. Hattenschwiler. 2014. Consequences of biodiversity loss for litter decomposition across biomes. Nature **509**:218-221.

Heath, G. W., C. A. Edwards, and M. K. Arnold. 1964. Some methods for assessing the activity of soil animals in the breakdown of leaves. Pedobiologia **4**:80-87.

Heinze, S., J. Raupp, and R. G. Joergensen. 2010. Effects of fertilizer and spatial heterogeneity in soil pH on microbial biomass indices in a long-term field trial of organic agriculture. Plant and Soil **328**:203-215.

Huhta, V., H. Setälä, and J. Haimi. 1988. Leaching of n and c from birch leaf litter and raw humus with special emphasis on the influence of soil fauna. Soil Biology and Biochemistry **20**:875-878.

Jansson, S. L. 1958. Tracer studies on nitrogen transformations in soil with special attentron to mineralization-immobilization relationships. Ann. R. Agric. Coll. Sweden **24**:101-361.

Klotzbücher, T., A. Marxen, D. Vetterlein, J. Schneiker, M. Türke, N. van Sinh, N. H. Manh, H. van Chien, L. Marquez, S. Villareal, J. V. Bustamante, and R. Jahn. 2015. Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. Basic and Applied Ecology.

Knapp, E. B., L. F. Elliott, and G. S. Campbell. 1983. Microbial respiration and growth during the decomposition of wheat straw. Soil Biology and Biochemistry **15**:319-323.

Koegel-Knabner, I., W. Amelung, Z. Cao, S. Fiedler, P. Frenzel, R. Jahn, K. Kalbitz, A. Kölbl, and M. Schloter. 2010. Biogeochemistry of paddy soils. Geoderma **157**:1-14.

Kurihara, Y. 1989. Ecology of Some Ricefields in Japan as Exemplified by Some Benthic Fauna, with Notes on Management. Internationale Revue der Gesamten Hydrobiologie **74**:507-548.

Lekha, A., G. Chopra, and S. R. Gupta. 1989. Role of soil fauna in decomposition of rice and sorghum straw. Proceedings of the Indian Academy of Sciences **98**:275-284.

Lepš, J., and P. Šmilauer. 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, New York.

Leyer, I., and K. Wesche. 2007. Multivariate Statistik in der Ökologie - Eine Einführung. Springer, Berlin Heidelberg New York.

Liang, W., X. Zhang, Q. Li, Y. Jiang, W. Ou, and D. A. Neher. 2005. Vertical Distribution of Bacterivorous Nematodes under Different Land Uses. Journal of nematology **37**:254-258.

Lønborg, C., and M. Søndergaard. 2009. Microbial availability and degradation of dissolved organic carbon and nitrogen in two coastal areas. Estuarine, Coastal and Shelf Science **81**:513-520.

Ma, J., and E. Takahashi. 1989. Release of silicon from rice straw under flooded conditions. Soil Science and Plant Nutrition **35**:663-667.

MacFadyen, A. 1961. Improved Funnel-Type Extractors for Soil Arthropods. Journal of Animal Ecology **30**:171-184.

Manzoni, S., R. B. Jackson, J. A. Trofymow, and A. Porporato. 2008. The Global Stoichiometry of Litter Nitrogen Mineralization. Science **321**:684-686.

Martinez, A., A. Larranaga, J. Perez, E. Descals, and J. Pozo. 2014. Temperature affects leaf litter decomposition in low-order forest streams: field and microcosm approaches. FEMS Microbiol Ecol **87**:257-267.

Merckx, R., A. den Hartog, and J. A. van Veen. 1985. Turnover of root-derived material and related microbial biomass formation in soils of different texture. Soil Biology and Biochemistry **17**:565-569.

Mueller, N. D., J. S. Gerber, M. Johnston, D. K. Ray, N. Ramankutty, and J. A. Foley. 2012. Closing yield gaps through nutrient and water management. Nature **490**:254-257.

Oksanen, J., R. Kindt, P. Legendre, B. O’Hara, M. H. H. Stevens, M. J. Oksanen, and M. Suggests. 2007. The vegan package. Community ecology package.

Perez, J., J. Galan, E. Descals, and J. Pozo. 2014. Effects of fungal inocula and habitat conditions on alder and eucalyptus leaf litter decomposition in streams of northern Spain. Microb Ecol **67**:245-255.

Rao, C. R. 1964. The use and interpretation of principal component analysis in applied research. Sankhyā: The Indian Journal of Statistics, Series A **26**:329-358.

Reddy, M. V., V. R. Reddy, D. F. Yule, A. L. Cogle, and P. J. George. 1994. Decomposition of straw in relation to tillage, moisture, and arthropod abundance in a semi-arid tropical Alfisol. Biology and fertility of soils **17**:45-50.

Saha, P. K., M. A. M. Miah, A. T. M. S. Hossain, F. Rahman, and M. A. Saleque. 2009. Contribution of rice straw to potassium supply in rice-fallow-rice cropping pattern. Bangladesh Journal of Agricultural Research **34**:633-643.

Santos, P. F., and W. G. Whitford. 1981. The Effects of Microarthropods on Litter Decomposition in a Chihuahuan Desert Ecosystem. Ecology **62**:654-663.

Schädler, M., and R. Brandl. 2005. Do invertebrate decomposers affect the disappearance rate of litter mixtures? Soil Biology and Biochemistry **37**:329-337.

Schädler, M., G. Jung, H. Auge, and R. Brandl. 2003. Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. Oikos **103**:121-132.

Schmidt, A., H. Auge, R. Brandl, K. L. Heong, S. Hotes, J. Settele, S. Villareal, and M. Schädler. 2015a. Small-scale variability in the contribution of invertebrates to litter decomposition in tropical rice fields. DOI: 10.1016/j.baae.2015.01.006. Basic and Applied Ecology.

Schmidt, A., K. John, G. Arida, H. Auge, R. Brandl, F. G. Horgan, S. Hotes, L. Marques, N. Radermacher, J. Settele, V. Wolters, and M. Schädler. 2015b. Effects of residue management on decomposition in irrigated rice fields are not related to changes in the decomposer community. DOI: journal.pone.0134402. PLOS ONE.

Setälä, H., J. Haimi, and V. Huhta. 1988. A microcosm study on the respiration and weight loss in birch litter and raw humus as influenced by soil fauna. Biology and fertility of soils **5**:282-287.

Settele, J., I. Kühn, S. Klotz, G. Arida, E. Bergmeier, B. Burkhard, and e. al. 2015. A cultural landscapes and ecosystems services in south-east Asia – The LEGATO-project. Basic and Applied Ecology.

Settle, W. H., H. Ariawan, E. T. Astuti, W. Cahyana, A. L. Hakim, D. Hindayana, A. S. Lestari, and Pajarningsih. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology **77(7)**:1975-1988.

Sileshi, G., and P. L. Mafongoya. 2006. Variation in macrofaunal communities under contrasting land use systems in eastern Zambia. Applied Soil Ecology **33**:49-60.

Simpson, I. C., P. A. Roger, R. Oficial, and I. F. Grant. 1993a. Density and composition of aquatic oligochaete populations in different farmers' ricefields. Biology and fertility of soils **16**:34-40.

Simpson, I. C., P. A. Roger, R. Oficial, and I. F. Grant. 1993b. Impacts of agricultural practices on aquatic oligochaete populations in ricefields. Biology and fertility of soils **16**:27-33.

Singh, Y., R. K. Gupta, J. Singh, G. Singh, G. Singh, and J. K. Ladha. 2010. Placement effects on rice residue decomposition and nutrient dynamics on two soil types during wheat cropping in rice–wheat system in northwestern India. Nutrient Cycling in Agroecosystems **88**:471-480.

Singh, Y., B. Singh, and J. Timsina. 2005. Crop residue management for nutrient cycling and improving soil productivity in rice-based cropping systems in the tropics. Advances in Agronomy **85**:269-407.

Steinberger, Y., and W. G. Whitford. 1988. Decomposition process in Negev ecosystems. Oecologia **75**:61-66.

Talbot, J. M., and K. K. Treseder. 2011. Ecology: Dishing the dirt on carbon cycling. Nature Clim. Change **1**:144-146.

Tengerdy, R. P., and G. Szakacs. 2003. Bioconversion of lignocellulose in solid substrate fermentation. Biochemical Engineering Journal **13**:169-179.

Tian, G., L. Brussaard, and B. T. Kang. 1993. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions: effects on soil fauna. Soil Biology & Biochemistry **25**:731-737.

Tian, G., L. Brussaard, and B. T. Kang. 1995. An index for assessing the quality of plant residues and evaluating their effects on soil and crop in the (sub-)humid tropics. Applied Soil Ecology **2**:25-32.

Tian, G., B. T. Kang, and L. Brussaard. 1992. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions - decomposition and nutrient release. Soil Biology & Biochemistry **24**:1051-1060.

Timsina, J., R. J. Buresh, A. Dobermann, and J. Dixon. 2011. Rice-maize systems in Asia: current situation and potential. International Rice Research Institute (IRRI) International Maize and Wheat Improvement Center, Los Baños (Philippines).

Timsina, J., M. Jat, and K. Majumdar. 2010. Rice-maize systems of South Asia: current status, future prospects and research priorities for nutrient management. Plant and Soil **335**:65-82.

Underwood, A. J. 1994. On Beyond BACI: Sampling Designs that Might Reliably Detect Environmental Disturbances. Ecological Applications **4**:3-15.

USDA. 2007. US Department of Agriculture. www.usda.gov.

van den Wollenberg, A. L. 1977. Redundancy analysis an alternative for canonical correlation analysis. Psychometrika **42**:207-219.

Vigil, M. F., and D. E. Kissel. 1991. Equations for Estimating the Amount of Nitrogen Mineralized from Crop Residues. Soil Science Society of America Journal **55**:757-761.

Wall, D. H., M. A. Bradford, M. G. St. John, J. A. Trofymow, V. Behan-Pelletier, D. E. Bignell, J. M. Dangerfield, W. J. Parton, J. Rusek, W. Voigt, V. Wolters, H. Z. Gardel, F. O. Ayuke, R. Bashford, O. I. Beljakova, P. J. Bohlen, A. Brauman, S. Flemming, J. R. Henschel, D. L. Johnson, T. H. Jones, M. Kovarova, J. M. Kranabetter, L. E. S. Kutny, K.-C. Lin, M. Maryati, D. Masse, A. Pokarzhevskii, H. Rahman, M. G. Sabar, J.-A. Salamon, M. J. Swift, A. Varela, H. L. Vasconcelos, D. O. N. White, and X. Zou. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Global Change Biology.

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological Linkages Between Aboveground and Belowground Biota. Science **304**:1629-1633.

Wardle, D. A., K. S. Nicholson, K. I. Bonner, and G. W. Yeates. 1999. Effects of agricultural intensification on soil-associated arthropod population dynamics, community structure, diversity and temporal variability over a seven-year period. Soil Biology and Biochemistry **31**:1691-1706.

Wassmann, R., and P. L. G. Vlek. 2004. Mitigating Greenhouse Gas Emissions from Tropical Agriculture: Scope and Research Priorities. Environment, Development and Sustainability **6**:1-9.

Watanabe, I., and P.-A. Roger. 1985. Ecology of flooded rice fields. Pages 229-243 Wetland Soils: Characterization, Classification, and Utilization, Los Baños, Philippines.

Weerakoon, A. C. J., and E. L. Samarasinghe. 1957. Mesofauna of the soil of a paddy-field in Ceylon - a preliminary survey. Ceylon Journal of Science (Biological Science) **1**:155-170.

Widyastuti, R. 2002. Soil fauna in rainfed paddy field ecosystems: their role in organic matter decomposition and nitrogen mineralization. Ecology and Development Series Band 3. Cuvillier Verlag, Göttingen.

Witt, C., K. G. Cassman, D. C. Olk, U. Biker, S. P. Liboon, M. I. Samson, and J. C. G. Ottow. 2000. Crop rotation and residue management effects on carbon sequestration, nitrogen cycling and productivity of irrigated rice systems. Plant and Soil **225**:263-278.

Witt, C., J. M. C. A. Pasuquin, R. Mutters, and R. J. Buresh. 2005. New leaf color chart for effective nitrogen management in rice. Better crops **89**:36-39.

Wolters, V. 1991. Soil Invertebrates - Effects on Nutrient Turnover and Soil Structure - A Review. Zeitschrift für Pflanzenernährung und Bodenkunde **154**:389-402.

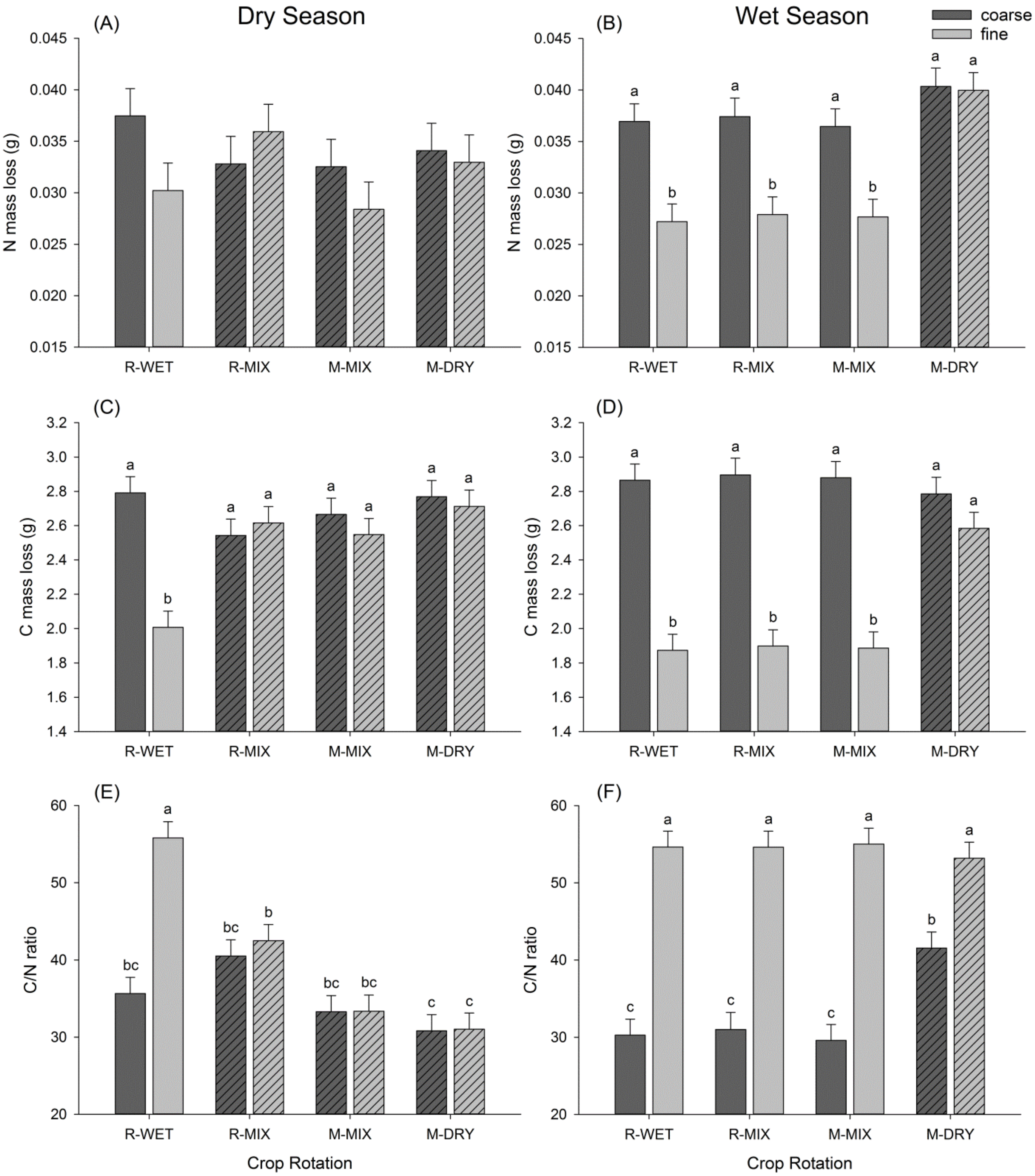
Yeates, G. W., T. Bongers, R. G. M. De Goede, D. W. Freckman, and S. S. Georgieva. 1993. Feeding habits in soil nematode families and genera - an outline for soil ecologists. Journal of nematology **25**:315.

SUPPLEMENTARY MATERIAL

S 1 The effects of *crop*, *fert* and *mesh* as well as their interactions on N and C mass loss and C/N ratios in rice straw using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Dry Season 2013	N mass loss (g)			C mass loss (g)			C/N ratio		
Factors	Df	F	*P*	Df	F	*P*	Df	F	*P*
crop	3,8	0.58	0.65	3,8	3.40	0.07	3,8	15.4	**0.001**
fert	2,16	0.08	0.92	2,16	0.26	0.77	2,16	2.44	0.12
mesh	1,24	3.21	0.09	1,24	15.3	**0.001**	1,24	24.6	**<.0001**
crop × *fert*	6,16	0.53	0.78	6,16	0.70	0.65	6,16	1.20	0.36
crop × *mesh*	3,24	2.85	**0.05**	3,24	11.5	**<.0001**	3,24	18.6	**<.0001**
fert × *mesh*	2,24	0.23	0.8	2,24	0.48	0.62	2,24	1.08	0.36
crop × *fert* × *mesh*	6,24	0.27	0.95	6,24	0.14	0.99	6,24	0.76	0.61
Wet Season 2013									
crop	3,8	6.41	**0.02**	3,8	3.06	0.09	3,8	2.24	0.16
fert	2,16	0.52	0.61	2,16	0.90	0.43	2,16	0.15	0.86
mesh	1,22	84.7	**<.0001**	1,22	405	**<.0001**	1,22	272	**<.0001**
crop × *fert*	6,16	0.38	0.88	6,16	0.41	0.86	6,16	0.47	0.82
crop × *mesh*	3,22	8.18	**0.001**	3,22	24.4	**<.0001**	3,22	6.42	**0.003**
fert × *mesh*	2,22	0.05	0.96	2,22	0.26	0.77	2,22	0.90	0.42
crop × *fert* × *mesh*	6,22	0.48	0.81	6,22	0.36	0.89	6,22	0.78	0.59

Factor *crop* represents the 4 different crop rotations (R-WET, R-MIX, M-MIX, M-DRY), factor *fert* the effect of the three different fertilizer treatments (zero, site specific, conventional), and factor *mesh* the two litterbag mesh sizes (5 mm and 20 µm) used in every plot. The model also includes the random effects of *field(crop)* (crop nested in field) and *fert* × *field(crop)*; their effects and interactions are not shown.



S 2 N and C mass loss and C/N ratios (means + SE) of rice straw litter in coarse- and fine-meshed litterbags retrieved from fields of the four crop rotations; A, C, E: dry season; B, D, F: wet season. Hatched bars constitute the aerobic variants in the particular season. Different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). For the N mass loss in the dry season the post-hoc test revealed no significant differences in means. C/N value of the original straw: C/N = 61.5.

S 3 The effects of *crop, fert* and *time* as well as their interactions on the ergosterol content in the soil (µg per g soil dry mass) using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Dry Season	Ergosterol (µg g^{-1})		
Factors	Df	F	*P*
crop	3,8	0.44	0.73
fert	2,16	3.17	0.07
time	1,24	76.3	**<.0001**
crop × *fert*	6,16	1.38	0.28
crop × *time*	3,24	5.35	**0.006**
fert × *time*	2,24	4.15	**0.03**
crop × *fert* × *time*	6,24	1.28	0.3

Factor *crop* represents the 4 different crop rotations (R-WET, R-MIX, M-MIX, M-DRY), factor *fert* the effect of the three different fertilizer treatments (zero, site specific, conventional), and factor *time* the effect of the two different points in time ergosterol content was measured (DS-end, WS-end). The model also includes the random effects of *field(crop)* (crop nested in field) and *fert* × *field(crop)*; their effects and interactions are not shown.

S 4 Eigenvalues of the six RDA axes and their contribution to the total variance as well as accumulated constrained ('Acc.') eigenvalues and contribution to the accumulated variation of the six RDA axes from the community analyses of soil faunal abundances.

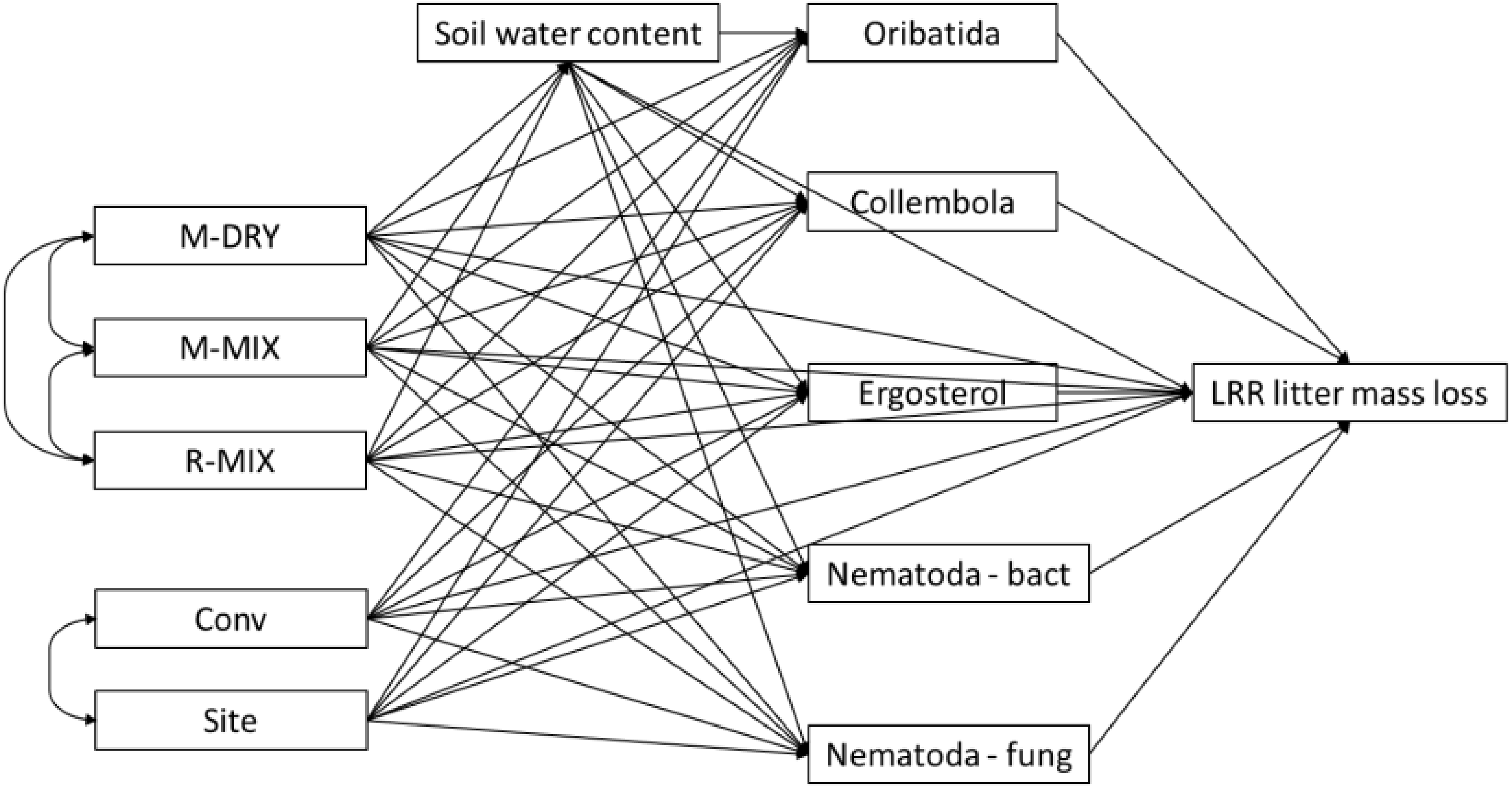
	RDA 1	RDA 2	RDA 3	RDA 4	RDA 5	RDA 6
Eigenvalue	2.3	1.04	0.33	0.24	0.11	0.04
Proportion explained (%)	8.2	3.7	1.19	0.87	0.38	0.16
Acc. eigenvalue	2.3	1.04	0.33	0.24	0.11	0.04
Acc. proportion explained (%)	56.6	25.6	8.19	6.01	2.62	1.08

S 5 Centroids for factor constraints of the first two RDA axes; highest absolute values are indicated in bold font.

	RDA 1	RDA 2
M-DRY	-0.38	0.27
M-MIX	0.09	-0.02
R-MIX	0.03	-0.25
R-WET	0.3	0.004
DS-end	**-0.9**	0.53
DS-start	-0.24	**-1.08**
WS-end	0.66	0.39
WS-start	0.48	0.16

S 6 ANOVA table of permutation tests for the six RDA axes and the constraining environmental variables *time* and *crop*. ‘Perm’ = number of permutations. Significant effects are indicated in bold font.

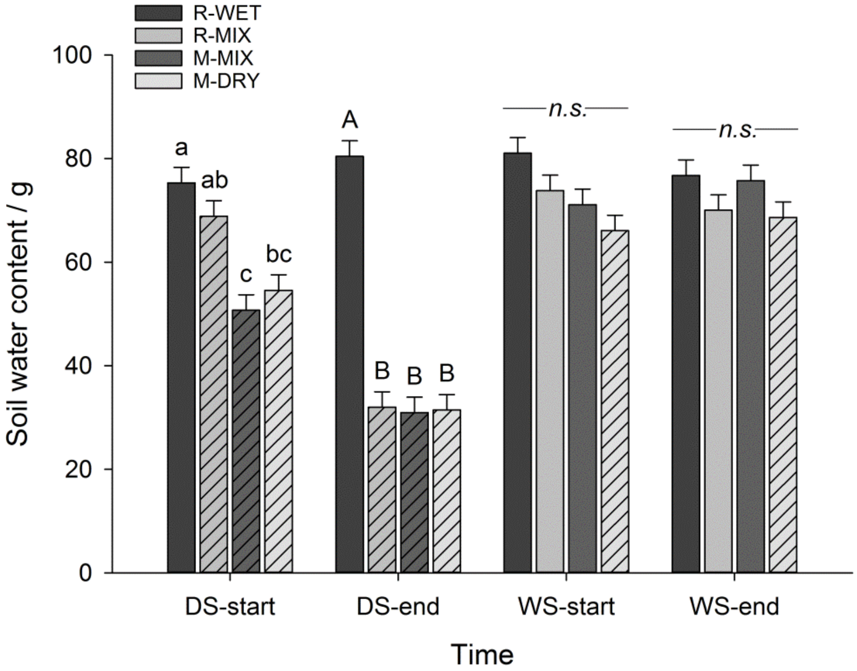
	Df	Var	Perm	F	*P*
RDA 1	1	2.30	199	13.1	**0.01**
RDA 2	1	1.04	199	5.93	**0.01**
RDA 3	1	0.33	199	1.90	**0.02**
RDA 4	1	0.24	599	1.40	0.08
RDA 5	1	0.11	99	0.61	0.95
RDA 6	1	0.04	99	0.25	1
Time	3	0.99	199	1.88	**0.01**
Crop	3	3.07	199	5.86	**0.01**



S 7 SEM - initial model (dry season); model fit indices: χ^2 = 8.7, Df = 18, *P = 0.97*, CAIC = 283.741; "Nematoda - bact" = bacterial feeding nematodes; "Nematoda - fung" = fungal feeding nematodes; "Conv" = conventional fertilization treatment; "Site" = site specific fertilization treatment; "LRR litter mass loss" = log response ratio of litter mass loss; "Collembola" = total abundance of all collembolan groups.

S 8 Standardized regression weights (Estimate (std)), unstandardized regression weights (Estimate), standard errors (SE) and critical ratio (C.R.) of fitted model. Significant relationships are indicated in bold font; *P ≤ 0.001****.

			Estimate (std)	Estimate	SE	C.R.	*P*
M-MIX	→	Soil water content	-1.00	-37.1	2.94	-12.6	***
M-DRY	→	Soil water content	-0.94	-34.9	2.94	-11.9	***
R-MIX	→	Soil water content	-0.74	-27.5	2.94	-9.33	***
M-DRY	→	Nematoda - bacterial feeding	-0.45	-3.28	0.99	-3.31	***
Site	→	Nematoda - bacterial feeding	0.40	2.71	1.05	2.59	**0.01**
Conv	→	Oribatida	0.26	753	395	1.91	0.06
Conv	→	LRR litter mass loss	-0.16	-0.07	0.04	-1.8	0.07
M-DRY	→	Oribatida	0.51	1565	429	3.65	***
Conv	→	Nematoda - bacterial feeding	0.35	2.33	1.05	2.22	**0.03**
Soil water content	→	LRR litter mass loss	0.72	0.01	0.001	7.8	***
Soil water content	→	Sum Collembola	-0.44	-66.6	21.6	-3.08	**0.002**
Conv	→	Sum Collembola	0.32	1632	733	2.23	**0.03**
R-MIX	→	LRR litter mass loss	-0.32	-0.16	0.04	-3.5	***



S 9 Soil water content (per g dry mass) per *crop* at the four sampling times (means + SE). Hatched bars constitute the aerobic variants in the particular season. Different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). Post-hoc comparisons were only made within one point in time, not between times.

S 10 The effects of *crop*, *fert* and *time* as well as their interactions on the soil water content (per g dry mass) using a GLMM type III sum of squares. Significant effects are indicated in bold font.

	Soil water content / g		
Factors	Df	F	*P*
crop	3,8	23.2	**0.0003**
fert	2,16	0.71	0.51
time	3,72	137	**<.0001**
crop × *fert*	6,16	0.76	0.61
crop × *time*	9,72	20.7	**<.0001**
fert × *time*	6,72	0.43	0.86
crop × *fert* × *time*	18,72	0.8	0.69

Factor *crop* represents the 4 different crop rotations (R-WET, R-MIX, M-MIX, M-DRY), factor *fert* the effect of the three different fertilizer treatments (zero, site specific, conventional), and factor *time* the effect of the four different points in time soil water content was measured (DS-start, DS-end, WS-start, WS-end). The model also includes the random effects of *field(crop)* (crop nested in field) and *fert* × *field(crop)*; their effects and interactions are not shown.

Chapter 5

RICE STRAW CONSUMPTION BY THE INVASIVE APPLE SNAIL *POMACEA CANALICULATA* (CAENOGASTROPODA, AMPULLARIIDAE)

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ABSTRACT

Only few studies test for the potential of invasive species, particularly pests, to contribute to ecosystem services. Apple snails of the *Pomacea-canaliculata* group are invasive in many countries around the globe. They are best known as pests of rice and taro and great efforts are made by farmers to decimate the number of snails. However, apple snails are also efficient decomposers of organic litter, and we assumed that they might enhance the decomposition of rice straw commonly incorporated into paddies by farmers for fertilization. To test the ability of apple snails to feed on rice straw, we conducted choice and no choice feeding experiments offering rice straw to *P. canaliculata* for 2 weeks. As mature rice plants are not consumed by apple snails, we incubated the straw with effective microorganisms for four different periods (5, 25, 50 and 75 days) prior to the feeding experiments. Rice straw of all different incubation times was partly consumed by snails (11.5 % more weight loss on average compared to controls where snails had no access). In another experiment we let snails feed on rice straw for 6 weeks; body mass and size of snails was measured weekly. All snails survived, body mass and size remained constant. Survival of snails fed with rice straw is much higher than on some aquatic weeds in other studies. We conclude that rice straw serves as an alternative food for apple snails. Invasive apple snails spared in times when rice plants are invulnerable could accelerate nutrient release from rice straw providing a benefit for farmers.

Keywords: golden apple snail, detritivores, *Oryza sativa*, rice field, effective microorganisms

INTRODUCTION

Most studies on the ecology of invasive species are intended to test potential negative impacts of the exotic species on native ecosystems, species or on ecosystem functions and services (Nentwig 2007). Invasive species, particularly pests of horticultural or agricultural plants, however, could also contribute to ecosystem services, if the right management actions are performed. To evaluate the potential of an invasive pest to contribute to the ecosystem function of decomposition associated with the ecosystem service of nutrient cycling in rice fields, we tested whether wide-spread invasive apple snails feed on rice straw in the laboratory.

Irrigated rice cultivation supplies the staple food for over one third of the world's population, and rice production is one of the most important and successful agricultural activities in Southeast Asia (Kurihara 1989). Farmers apply large amounts of mineral or organic fertilizers to increase their yields. Additionally, crop residues are often applied to the fields either untreated or as ash of burned straw (Samra et al. 2003, Singh et al. 2005, Hanafi et al. 2012). The rice straw plowed into the paddy soil is degraded by the decomposer community and nutrients are made available for the next cropping season (Fairhurst et al. 2007). Invertebrate decomposers play a key role in this decomposition process (Lekha et al. 1989, Wolters 1991, Schmidt et al. 2015). They break down bigger particles of dead organic material and make them available for micro-decomposers which release nutrients bound in plant tissues into the soil.

Decomposition is essential for enhancing or maintaining soil productivity and therefore crucial for plant growth (Tian et al. 1993). Some microorganisms involved in the decomposition of rice straw have already been identified, such as bacteria (Weber et al. 2001, Asari et al. 2007) and fungi (Abdulla and El-Shatoury 2007), but much less is known about the larger invertebrates processing the material for microbial decomposition. While experiments proved that earthworms, mites, springtails and millipedes do consume rice straw (Lekha et al. 1989, Tian et al. 1995), we found no information about gastropods, another prominent taxon of macro-decomposers, which are also very common and abundant in rice fields (Roger 1996). In terrestrial ecosystems gastropods are known to break down coarse plant material to smaller fragments making them accessible to digestion by microorganisms (Dallinger et al. 2001). Snails contribute to the decomposition of leaf litter also in aquatic environments (Mulholland et al. 1985, Slim et al. 1997, Kuehn and Suberkropp 1998, Proffitt and Devlin 2005, Tavares et al. 2011). Addition of rice straw to the flood water of rice fields strongly increased snail populations, indicating that straw might be used by snails as food (Roger 1996).

In the past decades, a number of apple snail species were introduced to water bodies outside their native range, either intentionally or unintentionally (Horgan et al. 2012). Among these snails two polyphagous, but mostly macrophytophagous species, *Pomacea canaliculata* Lamarck and *P. maculata* D'Orbigny (syn. *P. insularum* D'Orbigny), commonly referred to as golden apple snails or GAS, have become major pests in rice in SE-Asia where they can build up large populations (Cowie 2002). Rice seedlings are particularly vulnerable to the snails during the first weeks of their development until about two weeks after transplanting or four weeks after direct-seeding (Litsinger and Estano 1993). As rice plants mature they become unpalatable for the snails, which then mostly consume weeds in rice fields and, thus, can support weed control, reducing the efforts and costs of farmers for weed management (Okuma et al. 1994, Joshi et al. 2006). Alternatively, we hypothesize that snails might switch to a detritivorous feeding mode. To our knowledge, however, nothing is known about the impact of golden apple snails on decomposition processes of rice straw in paddies, although their role as detritivores was highlighted in other ecosystems (Tanaka et al. 2006, López van Oosterom et al. 2013). Invasive invertebrates can alter decomposition rates by direct consumption, displacement of litter from the soil surface into the soil matrix, facilitation of microbial decomposition or by changing the native decomposer community directly or indirectly (Ehrenfeld 2010). Evans (2012) found that invasive New Zealand mudsnails even played a bigger role in the breakdown and decomposition of riparian leaf litter in the invaded areas than native invertebrates. This could be true for golden apple snails in rice landscapes as well. As demonstrated for macrophyte consumption in natural wetlands in Thailand, snails strongly increase the concentrations of the plant growth-limiting nutrients phosphorus and nitrogen in the water (Carlsson et al. 2004), highlighting their potential to support fertilization of rice fields.

We hypothesized that the large, voracious golden apple snail *P. canaliculata* might consume rice straw and consequently contribute to straw decomposition in rice fields. Thus, due to their often very high abundance, *P. canaliculata* could also contribute significantly to nutrient availability in paddies. On the other hand, if *P. canaliculata* can use rice straw as alternative nourishment, crop residue management that involves leaving rice straw on the paddy could support large snail populations by enhancing survival during periods of food scarcity.

We conducted three experiments to answer the questions whether (1) *P. canaliculata* contributes to the decomposition of rice straw and whether the feeding activity interacts with the activity of litter-degrading microorganisms and (2) whether rice straw provides a suitable food source which allows survival and/or growth of the snails.

MATERIAL AND METHODS

Snails

Our study species was *Pomacea canaliculata* (Lamarck 1822), commonly referred to as golden apple snail (or GAS) in South-East Asia or as channeled apple snail in the USA. All experiments were conducted in the laboratory at the Technische Universität München, Freising, Germany (48°24ˈN, 11°43ˈE). We established populations of snails from eggs of different origins in the laboratory, which were kept separately to prevent cross-breeding. Snails of different origin had to be used in the experiments as the number of snails from any particular region was limited. Eggs (approximately 3 egg clusters each) were collected in rice fields in the Philippines at (1) the International Rice Research Institute (IRRI; Los Baños/ Laguna; 14°10ˈN, 121°15ˈE; collected 20 January 2012), (2) Batad (Banaue/ Ifugao; 16°56ˈN, 121°08ˈE; collected 20 March 2012) and (3) Bangaan (Banaue/ Ifugao; 16°54ˈN, 121°07ˈE; collected 21 March 2012). These rice fields were located at study sites of the LEGATO-project on land-use intensity and ecological engineering in irrigated rice (Klotzbücher et al. 2015; http://www.legato-project.net). In addition, the second generation of a lab population of *P. canaliculata* was used. Individuals of the parental generation were bought from a trader (Thorsten Krüger, Schanzenstr. 40, 90478 Nuremberg, Germany; http://www.krueger-aquaristik.de/). All snails were kept in glass aquaria measuring 29×29×35 cm (L×W×H; Aquael Deutschland GmbH Shrimp Set 30 L), covered with a glass lid and suited with a pat-mini filter (50 ÷ 400 l/h, 4 W), a heater (20 W; temperature was maintained at 22 to 25 °C) and lighting (fluorescent tube, 11 W; 12 hours/ day). Aquaria were provided with aquarium sand and a piece of sepia cuttlebone to provide calcium carbonate for the snails and were filled with approximately 25 l of tap water. About 6 l of the water were changed weekly. Snails were fed with various foods (mostly lettuce, vegetables, shrimp food, fish food and dried leaf litter) prior to the start of the experiments.

Plant material

The rice straw (*Oryza sativa*, variety NSIC Rc 222) used in the experiments originated from IRRI. It was obtained from rice plants harvested in the dry season of 2012 and oven-dried at 60 °C before being transported to Germany.

Pre-experimental incubation of rice straw

We assumed that consumption of straw by snails might be influenced by the degree to which it has been affected by microorganisms, and we tested this by incubating rice straw in water with added effective microorganisms for different periods of time. We established four treatments, each in a separate aquarium: microorganisms were added to treatments incubated for (1) 75 days (start on 31 October 2012), (2) 50 days (25 November 2012), and (3) 25 days (20 December 2012); in another treatment straw was incubated for (4) 5 days (10 January 2013) in tap water with no microorganisms added. This treatment was intended to test whether snails feed on freshly harvested rice straw, not pre-digested by microorganisms. Straw was transferred to tap water prior to the feeding experiments to allow it to soak up water and sink below the surface to achieve conditions similar to the other treatments. Rice straw was arranged in bundles of 3.04±0.02 g (mean±SD; N=50) and tied with plastic cable binders before incubation. Each bundle was placed in a polypropylene bag (35×20 cm L×W) with 1 mm holes. When bags were taken out of the aquaria, water drained through these holes ensuring that even small parts that might have fallen out of the straw bundles remained inside the bags. Rice straw was incubated in the same type of aquaria as described in the section on snails (see above), and temperatures were maintained at 29 to 30 °C. Right after transferring rice straw to an aquarium, we added 10 ml of effective microorganisms (eMB Aktiv Mikroorganismen, Multikraft Produktions- und HandelsgmbH, 4632 Pichl/Weis, Sulzbach 17, Austria; www.multikraft.com) to treatments 1 to 3. 'eMB Aktiv' consists of 5 % molasses, 90 % water and 5 % eMB concentrate, which is a mixture of photosynthetic and lactic acid bacteria (*Lactobacillus plantarum, L. fermentum, L. casei*), yeasts (*Saccharomyces cervisiae*) and other microorganisms for digesting hydrocarbons (fat and oil) and cellulose (*Athrobacter* spp., *Cellulomonas* spp.). The dilution we used is equal to the amount recommended by the producer for compost or waste water processing. Water was not changed during the incubation period. On 14 January 2013 rice straw bundles from all treatments were either used in the feeding experiments (see below) or were transferred to the drying oven at 60 °C for three days (treatment 1-3: 4 bundles each; treatment 4: 5 bundles) and weighed to the nearest centigram.

Experiment 1: choice experiment with straw incubated for different periods

On 14 January 2013 one bundle of rice straw from each of the four treatments was transferred to an aquarium (29×29×35 cm L×W×H; temperature 29-30°C) and fixed to the side of the aquarium, one treatment on each side (Fig. 1 a). The distribution of treatments was randomized in each of five replicates. The top of the bags was kept open with a plastic frame (9×12.5×6.5 L×B×H) to allow access by snails. The rim of the bags was located at 28 cm above the bottom of the aquarium and water was filled to a height of 31 cm so that snails could easily enter the bags without leaving the water. An additional bundle of rice straw incubated for 5 days in tap water was left in a closed bag to prevent access by snails and was fixed to the bottom in the center of the aquarium. These controls were established to compare microbial decomposition of the 5 day treatment in the choice experiment with the same treatment in the no-choice experiment (see below), as we expected that by transferring effective microorganisms attached to straw from treatments incubated for 25, 50 and 75 days to other aquaria, the microorganisms would colonize the straw previously not exposed to effective microorganisms, and that this would increase microbial decomposition during the experiment.

Ten snails from the same source population (Table 1) were added to each of the five aquaria on 15 January 2013. They were allowed to feed on the rice straw for 14 days until 29 January 2013, when the experiment was ended and all rice straw samples were dried and weighed. In this experiment, straw was collected together with feces from snails within bags and weighed together. Mean initial body mass of snails was 2.0 g, except for snails from Batad which were larger (Table 1). To investigate if snails were actually feeding on the rice straw, we observed the aquaria for 2 hours directly after the release of the snails on 29 January 2013, counting all snail individuals inside the bags of different treatments every 15 min (N=9 observations), categorizing their behavior as resting, active/moving and active/feeding on rice straw. In addition, we surveyed snail behavior once on each of the following days during the experiment: days 1 to 3, 6 to 10, 13 and 14 (n=10 days).

Experiment 2: no-choice experiment with straw incubated for different periods

In parallel with the choice feeding experiment, snails were also offered rice straw bundles of each of the four incubation treatments without choice (1 replicate each). Two rice bundles of the same treatment were transferred within bags to an aquarium and fixed to two opposite glass walls. One bag was opened to allow access by snails; the other one was closed without access by snails. This experiment was intended to provide information on two aspects: first, we wanted to quantify litter mass loss due to the action of microorganisms during the two week period of the feeding experiment (closed bags), to provide information needed to calculate the litter mass loss due to the activity of snails alone in the choice and in the no-choice experiment (experiment 1 and experiment 2, respectively). Second, in the choice experiment, certain treatments might completely be avoided by snails if other treatments are more attractive to them; thus, a no-choice experiment is necessary to test whether snails are able to feed on rice straw incubated for a certain time if this is the only food source available.

Ten snails were added to each aquarium on 15 January 2013 and were allowed to feed on the rice straw for 14 days until 29 January 2013, when the experiment was ended and all rice straw bundles were collected. In this experiment straw was collected together with feces from snails within bags and weighed together. The size distribution and origin of snails is shown in Table 1.

Experiment 3: survival experiment

This experiment was intended to monitor snail survival and growth with rice straw as the only food source over a longer period of time. Loose rice straw (10.04±0.01 g mean±SD) was incubated in bags in tap water with no effective microorganisms added (from 7 to 11 February 2013) as described above to allow the straw to soak up water and sink. Two bags each were then transferred to three aquaria (similar to the no-choice feeding experiment, but due to the longer duration of the experiment, a mini-filter was added to keep the water clean). One bag was closed to prevent access by snails serving as control and to quantify litter mass loss due to microorganisms which might be transferred to the aquaria with straw, snails or tap water. Five snails originating from IRRI were added to each aquarium on 12 February 2013. The cumulative weight of snails (body mass range 1.7 - 3.1 g) per replicate was between 11.16 and 11.83 g. Snails were marked individually and weighed before the experiment as well as weekly until the end of the experiment on 26 March 2013 (total duration of experiment 6 weeks). After removing the snails from the aquaria, they were blotted dry and water was released from the shells by pushing back the operculum before weighing. However, water inside the shell can account for some variance in body mass. We also measured shell height with digital calipers following Youens and Burks (2008). Rice straw was taken out on 26 March 2013, remaining straw and feces were separated (as we have learned from the choice and no-choice experiment where feces were not separated, that this will add another valuable information to understand and quantify rice straw decomposition by snails), dried and weighed as described above.

Data analyses

All statistical analyses were performed in R 3.1.2 (R Core Team 2014). For ANOVA we used the function *lm*, for Student's t-tests the function *t.test,* for general linear mixed models (GLMM) we used the function *lmer* in the 'lme4' package (Bates et al. 2014) together with the 'lmerTest' package (Kuznetsova et al. 2015), providing an analysis of variance table of type 3 with Satterthwaite approximation for degrees of freedom. For Tukey's HSD post-hoc tests we used the function *glht* in the 'multcomp' package (Hothorn et al. 2008). Count data was log-transformed. All figures were created using SigmaPlot 13.0 (Systat Software, Inc.).

Incubation with microorganisms

To identify which period of time during the incubation of straw with microorganisms over a maximum of 75 days is most important for litter mass loss, we compared the dry weight of rice straw after incubation using an ANOVA with incubation time (= 'treatment') included as the fixed factor.

Choice and no-choice experiment

To analyze the effect of snails on litter mass loss in the no-choice experiment, litter mass loss of rice straw from different incubation treatments with access by snails (open bags, N=1 replicate/ treatment) was compared to rice straw where snails had no access (controls, closed bags, N=1 replicate/ treatment) using a paired t-test, i.e. all four incubation treatments were included in this test but comparisons were made within treatments.

Litter mass loss of rice straw of different incubation treatments offered to snails in the choice experiment was compared using a GLMM with 'treatment' included as the fixed factor and 'replicate' as the random factor. Differences in litter mass loss, however, do not indicate preferences of snails for certain treatments. As 3 g of rice straw was incubated for a different period of time depending on the incubation treatment, a different amount of straw was remaining after incubation time and microbial decomposition. Thus, the weight of straw from different incubation treatments offered to snails in the feeding experiments differed. Therefore, we compared the dry weight of rice straw after the experiments, i.e. the amount of straw eaten by snails, to find preferences of snails for certain incubation treatments. To assess straw consumption by snails, we had to take microbial decomposition that was continuing during the two weeks of the feeding experiments into account and calculated straw consumption by snails as: dry weight of straw of treatment j without access by snails at the end of the feeding experiment (controls, closed bags in no-choice experiment, N=1 replicate/ treatment) minus dry weight of straw of replicate i of treatment j with access by snails at the end of the feeding experiment (open bags in the choice-experiment: N=5 replicates/ treatment and also in the no-choice experiment: N=1 replicate/ treatment). For the 5 day treatment, however, we could not use the control from the no-choice experiment to calculate straw consumption in the choice experiment as we introduced effective microorganisms to aquaria with straw of the other treatments in this experiment, but not in the 5 day treatment of the no-choice experiment. We found that litter mass loss of the 5 day controls was significantly higher in the choice experiment (5 replicates; 26±0.7 % mean±SD litter mass loss) than in the no-choice experiment (1 replicate; treated as the theoretical mean; 21 % litter mass loss) (t-test for one sample, df = 4, t = 17.30, $p < 0.001$). Thus, we used the mean of the controls from the choice experiment to calculate straw consumption of the 5 day treatment by snails there.

To find preferences of snails for rice straw of different incubation treatments in the choice experiment, a GLMM was used to compare dry weight of straw consumed by snails with 'incubation treatment' included as the fixed factor and the 'replicate' included as the random factor.

In the no-choice experiment, rice straw of only a single incubation treatment was offered to snails per replicate/ aquarium. Thus, snails were expected to consume more rice straw of this treatment than of the same treatment in the choice-experiment, where snails could feed on straw of four different treatments, but a similar amount of straw should be consumed in the no-choice experiment as the cumulative amount of straw of all treatments consumed in the choice experiment. To test if a higher amount of rice straw per treatment was consumed by snails in the no-choice experiment (1 replicate/ treatment) and the choice experiment (5 replicates/ treatment), we performed t-tests comparing the dry weight of rice straw of treatment i from the choice experiment against a theoretical mean, where we used the dry weight of straw of treatment i with access to snails from the no-choice experiment. Similarly, we performed an unpaired t-test comparing the cumulative dry weight of rice straw consumed by snails from all treatments per aquarium in the choice experiment (N=5 replicates) with the dry weight of straw consumed by snails per aquarium in the no-choice experiment (N=4 replicates).

Further, to identify a shift in preferences of snails for rice straw incubated for different periods of time, we compared the number of snails observed in bags of the different incubation treatments in the choice experiment on eleven days during the experiment. On the first day of the experiment, when nine observations were made, we used the rounded mean of snails observed within treatments. The number of snails in each treatment, added up for all five replicates, was analyzed using a GLMM with 'treatment', the 'days' after the start of the experiment on which observations were made and the interaction of both factors included as the fixed factors and the 'date of observation' as the random factor.

Survival experiment

We compared litter mass loss due to snail consumption (open bags) after six weeks with litter mass loss by leaching and microbial decomposition (controls, closed bags) using a paired t-test. Note that no commercial effective microorganisms were added to aquaria, but microorganisms will likely be introduced to aquaria along with rice straw, snails or tap water. Further, we compared live body mass and shell height of snails at the start of the experiment with weekly measurements using paired t-tests. As no snails died during the six week experiment, no statistical test was performed on the survival of snails.

RESULTS

Leaching and microbial decomposition

Incubation in water or in water with effective microorganisms added for a maximum of 75 days caused a high litter mass loss in rice straw ranging from 20.66 % to 58.28 % (5 day incubation and 75 day incubation, respectively) (Fig. 2 a). After 75 days of incubation most of the fine, filamentous parts of the straw were decomposed. We found significant differences in dry weight after incubation among treatments (ANOVA; $F_{3,13}$= 120.09, p<0.001). Dry weight was significantly different between all treatments as indicated by Tukey's HSD, except for the 25 day and the 50 day treatment (Fig. 2 a). Note that in contrast to the other treatments, no additional effective microorganisms were added to the 5 day treatment, but microorganisms might have been introduced to aquaria with straw or tap water. Excluding the 5 day treatment from the analysis, did not change results for the other treatments.

Rice straw consumption by snails

We observed snails feeding on rice straw (Fig. 1 b, c) of all treatments in all experiments, either pre-digested by effective microorganisms or incubated in tap water only, during the entire period of all experiments. In none of the treatments or replicates of any experiment rice straw was decomposed or consumed completely at the end of the experiments. Defecated fragments were small (less than 5 mm length) and thin (less than 0.5 mm thickness) sticks. Dried and stuck together they have a texture like rough paper (Fig. 1 d).

In the no-choice feeding experiment, rice straw had lost significantly more weight after two weeks if snails had access to straw (53.44±19.02 %, mean±SD) than rice straw where snails had been excluded (43.43±16.32 %), independent of the treatment, i.e. the period of time rice straw was incubated prior to the feeding experiment (paired t-test, df=3, t=4.39, p=0.0218; Fig. 2 c). Snail feces within bags were weighed together with the remaining straw in this experiment. Thus, effective litter mass loss of straw with access by snails can be assumed to be even higher. Therefore, our experiment provides a rather conservative estimate of the contribution of snails to the decomposition process. Similar to the no-choice feeding experiment, rice straw with access by snails lost significantly more weight (73.25±10.70 %, mean±SD) than straw without access by snails (46.64±6.57 %) during the six weeks of the survival experiment (paired t-test, df=2, t=-6.38, p=0.0237). Feces from feeding bags had been collected separately in this experiment and they were considered as litter mass being lost due to decomposition. With an average weight of 1.37±0.35 g feces accounted for 13.61±3.44 % of the initial weight of the rice straw. If feces were not treated as litter mass being lost due to decomposition, there was no significant difference in litter mass loss between straw with or without access by snails (paired t-test, df=2, t=3.73, p=0.0649).

Snail preferences (choice and no-choice experiment)

We found significant differences in litter mass loss according to the initial amount of straw (3.04 g on average) among treatments at the end of the choice experiment (GLMM; $F_{3,16}$= 46.69, p<0.001). Dry weight was significantly different between all treatments as indicated by Tukey’s HSD, except for the 25 day and the 50 day treatment (Fig. 2 b). To identify preferences of snails for rice straw incubated in water with effective microorganisms for different periods of time prior to the feeding experiments, we compared the amount of straw per treatment consumed by snails in the choice experiment (for calculation see materials and methods). Snails did not prefer straw from certain treatments over others, but consumed similar amounts of straw of the four different treatments (GLMM, $F_{3,16}$=3.16, p=0.053; Fig. 3).

Comparing the total amount of rice straw consumed per aquarium by snails between the no-choice experiment and the choice experiment, in contrast to our expectations, significantly less rice straw was consumed by snails in the no-choice experiment (0.29±0.13 g, mean±SD) than in the choice experiment (1.42±0.06 g) (t-test, df=4.05, t=18.90, p<0.001), although the same number of snails was used in both experiments. Similar amounts of rice straw of each of the four different incubation treatments were consumed in the choice and the no-choice experiment (t-tests for one sample; df=4, p>0.05).

On average, 44±5 % (mean±SD, range 32 – 52 %) of all snails were observed within feeding bags per day in the choice experiment, counted on eleven days during the 14 days of the experiment. We found no significant differences in the number of snails in feeding bags among treatments (GLMM, $F_{3,36}$= 2.05, p=0.125) or in the course of the experiment, i.e. the days after the start of the experiment on which observations were made ($F_{1,36}$= 0.62, p=0.435), but there was a significant interaction between the treatments and the days ($F_{3,36}$= 4.83, p=0.00632). We observed that more snails were attracted by the 50 day and 75 day incubation treatments than by the other treatments directly after the onset of the experiment (Fig. 4). Already after one day, however, fewer snails were observed in the 50 day treatment and the same was true after two days for the 75 day treatment. The 25 day treatment was attractive on the second day as well, but afterwards most snails were always observed in the 5 day treatment.

Snail performance (survival experiment)

All snails survived and remained active during the six weeks of the experiment with rice straw as the only food source. No eggs were deposited. There was no difference in body mass of the snails at the start of the experiment and at any of the weekly measurements (paired t-test, df=14, p>0.05), except for the measurement after two weeks where body mass had increased by 2.5±4.4 % (mean±SD; N=15) (t= 2.53, p=0.0240). Body mass at the start of the experiment was 2.30±0.41 g and 2.28±0.37 g at the end of the experiment. Changes in body mass at weekly measurements compared to the initial weight ranged from -9.85 % to 16.09 %

(0.98±4.53 %, mean±SD; N=90), which, however, could probably at least partly be attributed to inaccuracy in the measurement procedure, i.e. the amount of water remaining inside shells after manually releasing it. Therefore, we compared the body mass of snails before and after manually releasing the water from shells (N=15 snails). Snails weighed before water release from shells were 8±5 % (range 2 – 15 %) heavier than afterwards. Similar to body mass, there was no difference in shell height of the snails at the start of the experiment and at any of the weekly measurements (paired t-test, df=14, $p>0.05$), except for the measurement after one week where shell height was measured to be 1.8±1.9 % greater ($t= 3.63$, $p=0.00274$). Shell height at the start of the experiment was 14.87±1.07 mm and 14.93±0.93 mm at the end of the experiment. We noted fluctuations in shell height ranging from -5.58 to 5.29 % (0.07±2.32 %, mean±SD; N=90), which are most likely caused by inaccuracy, i.e. the exact positioning of calipers to measure shell height, as it is very unlikely that shells will decrease in size.

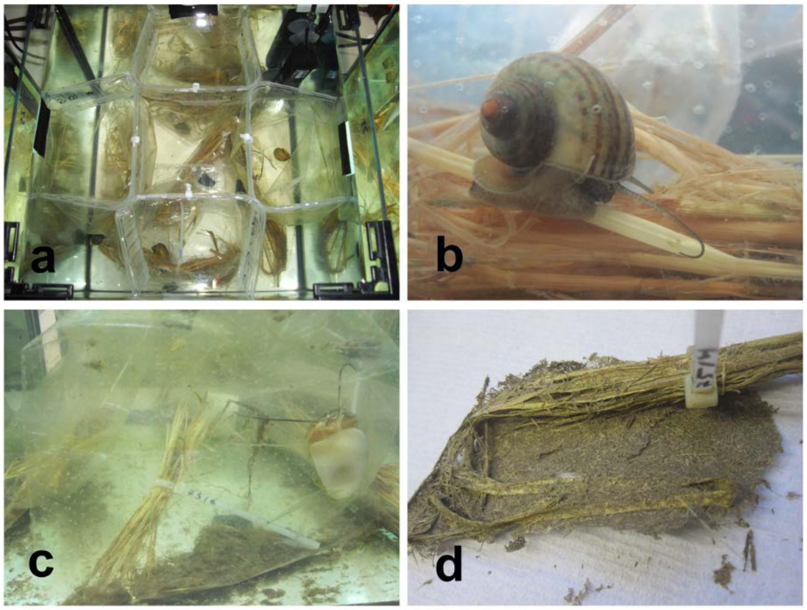

Fig. 1 (a) Setup of the choice feeding experiment, (b) *Pomacea canaliculata* feeding on rice straw, (c) rice straw and snail feces in a feeding bag, (d) dried rice straw together with feces after being offered in the feeding experiment. Photos by M. Türke

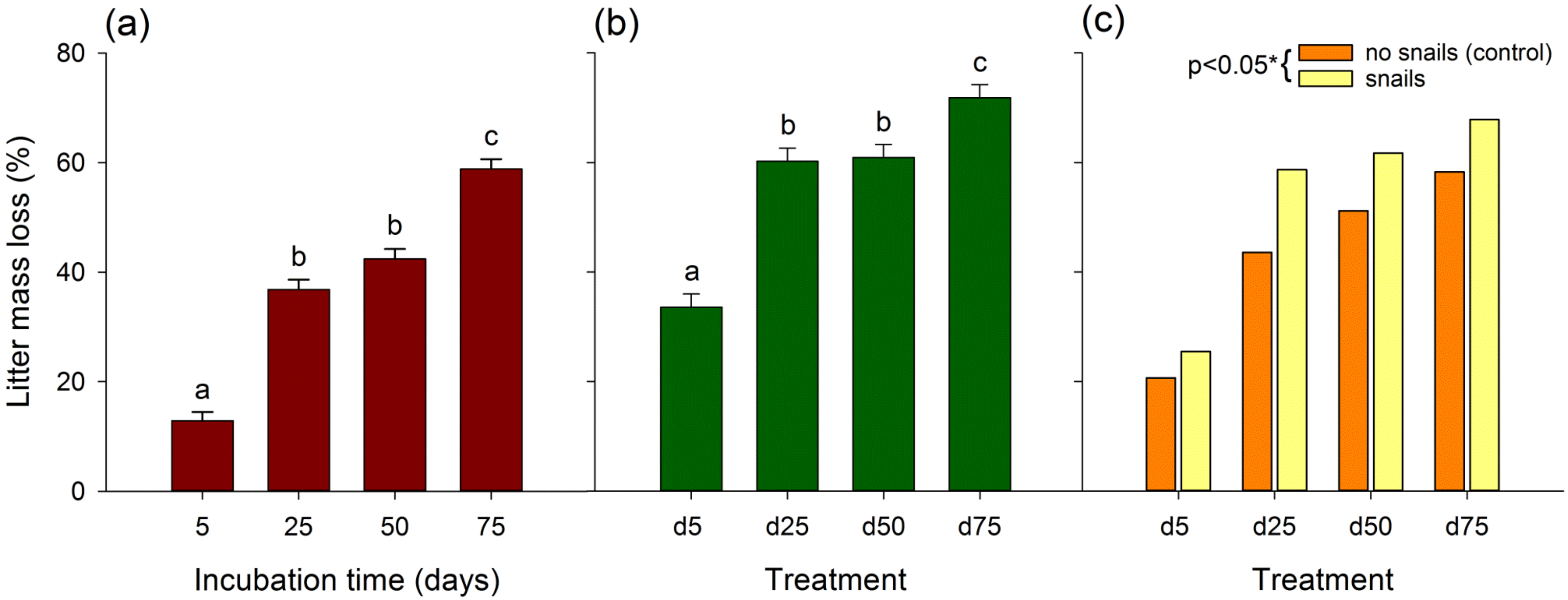

Fig. 2 Litter mass loss of rice straw (mean±SE) caused by leaching and microbial decomposition or by the interaction of microbes and straw consumption by snails. Prior to feeding experiments rice straw was incubated in tap water for 5 days (5d) or in tap water with effective microorganisms added for 25 (25d), 50 (50d) and 75 days (75d). (a) Microbial decomposition: a subset of the 3 g straw samples was dried and weighed after incubation (25, 50 and 75 days N=4 samples, 5 days N=5 samples). (b) Choice feeding experiment: in each replicate snails were allowed to feed on straw of all incubation treatments, i.e. straw incubated for different periods of time prior to the feeding experiments (N=5 replicates/ treatment). (c) No-choice feeding experiment: in each replicate there was straw of only one incubation treatment, one sample of rice straw with access to snails (= *snails*, N=1 replicate/treatment) and one sample without access by snails (= *control (no snails)*, N=1 replicate/treatment). A contribution of snails to rice straw decomposition is obvious; different letters within panels (a) and (b) indicate significant differences between treatments (GLMM followed by Tukey's HSD, $p<0.01$) and in (c) results of a paired t-test are shown.

Table 1 Body mass distribution of snails used in the feeding experiments. Ten snails were used in each experiment. "Sum" refers to the cumulative body mass of all snails in an aquarium.

			Body mass (g)				
Experiment	Replicate	Origin	Min	Max	Mean	SD	Sum
Choice	1	IRRI	1.2	2.8	2.1	0.5	19.2
Choice	2	IRRI	1.7	2.8	2.2	0.3	19.5
Choice	3	IRRI	0.9	2.8	2.0	0.5	18.9
Choice	4	Batad	2.2	8.7	4.6	2.5	42.8
Choice	5	Bangaan	1.7	2.9	1.9	0.4	17.6
No-choice	5 days	Trader	0.6	6.2	2.2	1.9	21.3
No-choice	25 days	Trader	0.6	8.1	2.4	2.5	23.8
No-choice	50 days	Trader	0.5	7.1	2.5	2.6	24.1
No-choice	75 days	Trader	0.4	7.9	2.7	2.5	26.2

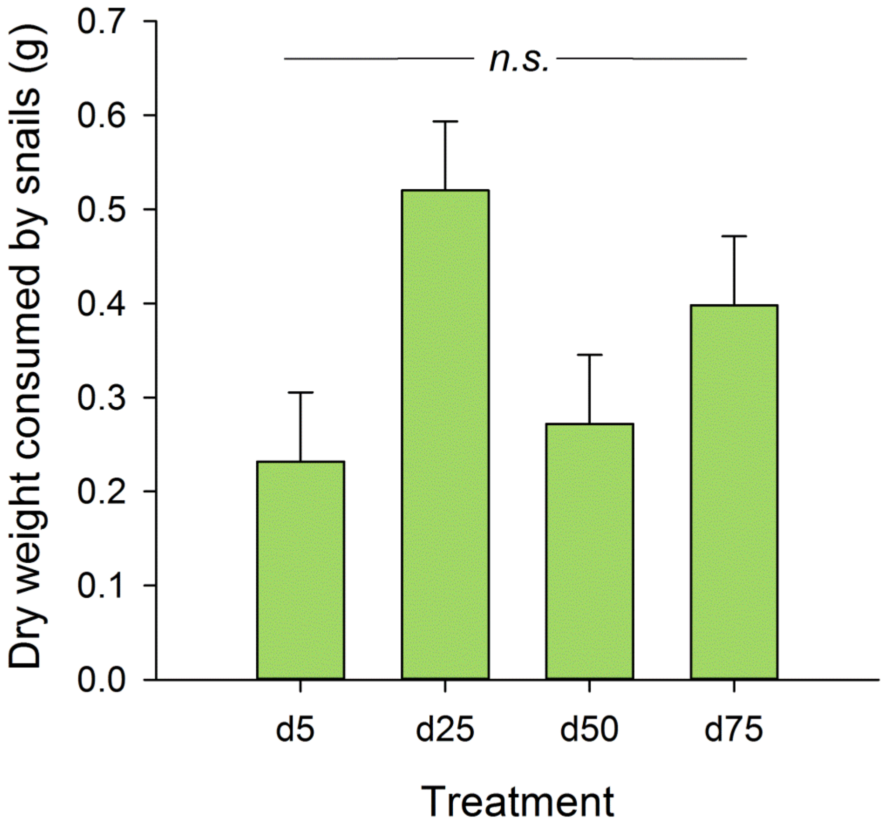

Fig. 3 Dry weight of rice straw consumed by snails of the four different incubation treatments in the choice feeding experiment. Results are given as mean±SE. There were no significant differences among treatments (GLMM, $p>0.05$).

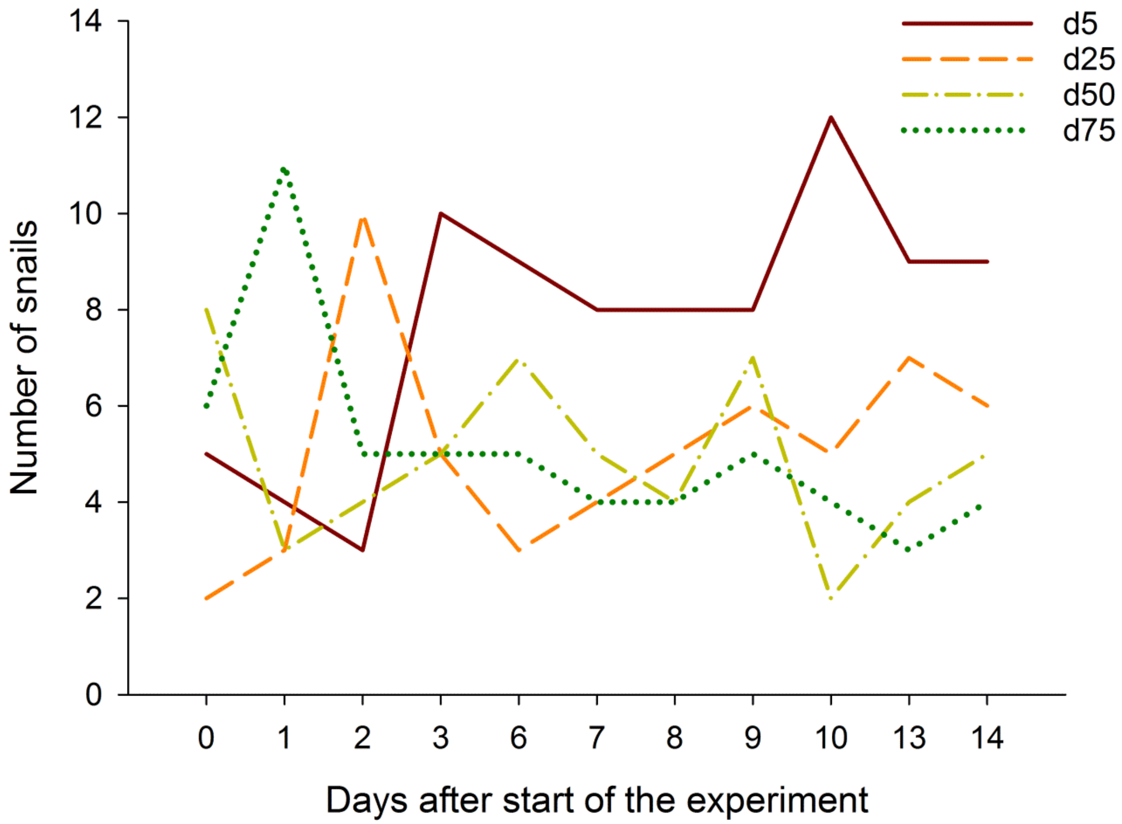

Fig. 4 Proportion of snails observed in bags containing rice straw incubated for 5, 25, 50 and 75 days, counted on 11 days during the 14 days of the choice feeding experiment. Only snails within bags were considered. On the first day of the experiment (day 0) snails were counted nine times in 15 min intervals and the mean of all counts is shown here. There is a shift in the preference of different incubation treatments by snails over time as also indicated by a significant interaction term of days and treatment (GLMM, $p<0.01$).

DISCUSSION

The invasive agricultural pest snail *Pomacea canaliculata* was described as a macrophytophagous species in a number of studies, feeding primarily on vegetal material of various plant species (e.g. Estebenet 1995, Lach et al. 2000, Qiu and Kwong 2009). In contrast to most other studies, it was found to mainly feed on detritus in a stream ecosystem in Argentina, where vegetal matter and diatoms were consumed less frequently by the snail (López van Oosterom et al. 2013). If they can utilize senescent plants or leaf litter, however, was rarely studied experimentally (but see Qiu et al. 2011). In our experiments, we tested whether *P. canaliculata* is feeding on rice straw, which is often incorporated into paddies for fertilization (Singh et al. 2005), and could thus act as an important decomposer in rice fields. We found that *P. canaliculata* significantly increased litter mass loss by feeding on the rice straw compared to control treatments where snails had no access. We conclude that invasive apple snails might be important decomposers of rice straw and thus contribute to the nutrient turnover in paddies.

Leaching and microbial decomposition

We noticed high litter mass loss during incubation of rice straw in water with effective microorganisms added (Fig. 2 a). However, litter mass also decreased by 13 % in treatments incubated for five days in tap water with no effective microorganisms added. This mass loss can most likely be attributed to the abiotic process of leaching. Leaching occurs directly after exposure of litter to water and lasts for a couple of days or weeks and it commonly accounts for a substantial litter mass loss due to the release of carbon, nitrogen and phosphorus (Ibrahima et al. 1995, Davis et al. 2006). Flushing rice straw under water accounted for an immediate mass loss of 5 % (Jenkins et al. 1996). Leaching in rice straw primarily reduces potassium, sodium, chlorine, alkali acids and ash concentration (Jenkins et al. 1996). Microorganisms can decrease some organic compounds, mostly carbohydrates, very quickly within a few days after exposure to rice straw, which, however, accounts for a minor litter mass loss only (Chen et al. 2010). In general, microorganisms were found to have limited influence on rice straw decomposition in flooded paddy fields due to the prevalent anaerobic conditions (Koegel-Knabner et al. 2010). We found no significant difference in litter mass loss between straw incubated for 25 and for 50 days, but a higher increase in litter mass loss after 75 days (Fig. 2 a). This could probably be related to changes in physical or chemical properties of straw over time with changes in the composition and biomass of different microorganisms and related microbial decomposition. Lu et al. (2003) found a linear increase in microbial biomass in soils incubated with rice straw in the first 150 days of incubation. We want to emphasize that we cannot differentiate between litter mass loss due to microbial decomposition and due to leaching.

Rice straw consumption by snails

In the choice and no-choice experiments, 11±6 % of the initial dry weight of rice straw (mean±SD; range 2 – 17 %) was consumed by snails after two weeks (with snail feces not regarded as litter mass lost). In the survival experiment, litter mass loss (with fecal material considered as litter mass lost) after six weeks was 26.61 % higher in treatments where snails had access (73.25 % of total litter mass) than in controls (46.64 %). This effect of golden apple snails on rice straw decomposition found in our experiment was at least as large as that of other macro-decomposers tested in the laboratory. Tian et al. (1995) found that earthworms increased the loss in rice straw mass after four weeks by 5.3 %, millipedes by 27.8 % and both together even by 36.4 % compared to controls. While we did not test for synergistic effects with other species, it is likely that invasive apple snails will also show synergitic effects with other groups of decomposers.

It may have been expected that the snails avoid freshly harvested rice straw from mature plants because live mature plants are unpalatable for the snails, most likely because silica has hardened the culms (Litsinger and Estano 1993). This assumption implies that feeding inhibitors are not lost due to leaching after exposure of straw to water. Silicon in litter, however, is partly leached and is also degraded by microorganism (Schaller and Struyf 2013). Therefore, we incubated rice straw for varying periods of up to 75 days in water with effective microorganisms added to pre-digest rice straw, potentially making it more palatable to the snails, e.g. hemicelluloses and cellulose are decomposed by microorganisms within the first nine weeks (Chen et al. 2010). We found that snails were feeding on straw independent of incubation time; differences in the amount of straw consumed that was either incubated in tap water for five days or for a longer period together with effective microorganisms were not significant (Fig. 3). On the other hand, we found a shift in the attractiveness of straw to snails in the choice experiment: straw incubated with effective microorganisms for a longer time attracted more snails at the beginning of the experiment than straw incubated for a shorter time or straw incubated without effective microorganisms, which, however, was most attractive a few days after the onset of the experiment (Fig. 4). In addition, we would have expected that snails will consume similar amounts of straw in total in the choice experiment, where snails could feed on all four treatments, and in the no-choice experiment, where snails had access to only one treatment, especially as straw was not consumed completely in any replicate of both experiments. However, snails in the no-choice experiment consumed on average only 15 mg dry weight of straw per individual and week, whereas 71 mg straw was consumed in the choice experiment. These results suggest that there was only a certain amount of easy degradable straw in each straw bundle that could be eaten by snails. Therefore, the observed shift in attractiveness and the discrepancy in the total amount of straw consumed between experiments could be that snails prefer some fine, filamentous parts of straw rather than thick holms and as these parts are eaten they will move on to the next favored treatment and consume the fine parts there and so on. As soon as all the fine parts are consumed the straw becomes unattractive to or unpalatable for the snails. However, we observed that in the 50 day and 75 day treatment most of these fine parts had already been digested by microorganisms prior to the feeding experiments. Our results provide indications for an alternative hypothesis though, i.e. that the microorganisms on straw themselves might be attractive food for the snails and are probably at least partly responsible for rice straw consumption. Biomass of microorganism colonizing straw will be greatest in the treatments incubated for a longer time (Lu et al. 2003). After consuming microorganisms on these treatments, snails might have moved on to consume microorganisms on straw of the other treatments. If snails mainly feed on microorganisms colonizing straw rather than straw itself, once the microorganisms are grazed by snails, regrowth of microorganisms will limit snail feeding.

In the survival experiment we also used straw incubated for 5 days without effective microorganism added. Snails consumed 44 mg per individual per week, thus, less straw was consumed per individual than in the choice experiment, but more than in the no-choice experiment. However, we used only five snails instead of ten snails in this experiment and provided a greater amount of rice straw with a longer duration of the experiment, potentially allowing for the establishment of populations of microorganisms and the regrowth of consumed microorganisms over time. If microorganisms on rice straw stimulate feeding by snails, we could expect that feeding rates will be higher in rice fields, where a diverse community of microorganisms instantly colonizes rice straw plowed into the soil (Weber et al. 2001, Abdulla and El-Shatoury 2007, Asari et al. 2007), compared to our experiments, where the amount (as related to the amount of straw that could be colonized) and species of microorganisms was limited. While it is known that some freshwater gastropods, e.g. lymnaeids, are feeding on bacteria (Dillon 2004), we could not find any information that ampullarids, and *P. canaliculata* in particular, are intentionally feeding on microorganisms (e.g. Dillon 2004, Joshi and Sebastian 2006). Therefore, designing our study, we did not consider the possibility that microorganisms colonizing rice straw could influence the feeding behavior of *P. canaliculata,* either stimulating or decreasing rice straw consumption and we will have to leave the confirmation or refutation of our assumptions to future studies.

Performance of snails feeding on rice straw

All snails survived and remained active over a period of six weeks with rice straw as the only food source in the survival experiment. However, after six weeks snails did not gain weight, increased in shell height or deposited eggs. A positive effect of leaf litter on survival of snails has been reported before. Qiu et al. (2011) kept *P. canaliculata* on diets of three macrophytes with either fresh or decaying leaves and measured shell growth and survival for one month. While juveniles of less than 2 cm shell length showed a significant increase in shell size on most of the food types offered, similar to our results, they found no or only marginal shell increment for snails larger than 2 cm (approximately the same size as most snails in our experiment). Survival, however, was lower in their experiments ranging from 40 to 90 %, whereas no snails died within the six weeks of our experiment. Survival of golden apple snails without food over a period of six weeks is very low. Lach et al. (2000) raised snails on different macrophytes and also without food. Only about 30 % of the unfed individuals survived until week six (ranging from 0 % to about 70 % depending on the replicate) and the authors assumed that the snails might have had access to some food from surface deposits such as algae. Survival and also growth were generally higher when fed on diets of single plant species. Fed with water hyacinth, *Eichhornia crassipes*, however, snails also faced high mortality of almost 70 % in 6 weeks and increased in size only slightly more than unfed individuals. Thus, we assume that rice straw can be considered as food that at least allows survival of snails for a longer period of time. In addition, considering survival of snails rice straw is probably of higher quality than some common aquatic weeds growing in the invasive range of *P. canaliculata* in SE-Asia or Hawaii (Lach et al. 2000, Qiu and Kwong 2009, Qiu et al. 2011). Finally, regarding our assumptions on the importance of microorganisms colonizing rice straw on the feeding behavior of snails, performance of snails might have even been better and the amount of rice straw consumed higher, if we had introduced effective microorganisms into aquaria.

Application

It was found that golden apple snails contribute to the ecosystem service of weed control in rice fields (Okuma et al. 1994, Joshi et al. 2006). Our results suggest that there is an additional ecosystem service, namely the breaking up of rice straw in the decomposition process, resulting in an increased or faster release of nutrients. On the other hand, rice plant residue management by farmers will have a direct effect on the performance of the invasive apple snails. Straw incorporated into the soil can serve as a food source for the snails especially in times of food shortage. This is likely to reduce mortality during fallow periods, which can result in higher densities of the pest snails at the beginning of the next cropping season when newly transplanted or sown rice plants are especially vulnerable to snail herbivory. Alternatively, if rice straw is burned and ash is applied on paddies, nutrients will be lost and the atmosphere gets polluted (Hanafi et al. 2012). Rice straw ash has, however, a lethal effect on golden apple snails (Cuevas et al. 1993). Thus, if farmers suffer from high snail damage, they might prefer to burn rice residues and apply ash on the field instead of plowing the straw into the soil. On the other hand, supporting the snails in times when rice is not growing or not vulnerable, farmers could benefit from a higher nutrient turnover in their fields if they use the method of straw fertilization.

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REFERENCES OF CHAPTER 5

Abdulla, H. M., and S. A. El-Shatoury. 2007. Actinomycetes in rice straw decomposition. Waste Management **27**:850-853.

Asari, N., R. Ishihara, Y. Nakajima, M. Kimura, and S. Asakawa. 2007. Succession and phylogenetic composition of eubacterial communities in rice straw during decomposition on the surface of paddy field soil. Soil Science and Plant Nutrition **53**:56-65.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Carlsson, N. O. L., C. Bronmark, and L. A. Hansson. 2004. Invading herbivory: The golden apple snail alters ecosystem functioning in Asian wetlands. Ecology **85**:1575-1580.

Chen, H.-L., J.-M. Zhou, and B.-H. Xiao. 2010. Characterization of dissolved organic matter derived from rice straw at different stages of decay. Journal of Soils and Sediments **10**:915-922.

Cowie, R. H. 2002. Apple Snails (Ampullariidae) as Agricultural Pests: their Biology, Impacts and Management. Pages 145-193 *in* G. M. Barker, editor. Molluscs as crop pests. CAB International, Wallingford.

Cuevas, S. C., A. R. R. Banatin, and M. N. G. Pua. 1993. Lethal effects of rice straw ash on golden snails. Bato Balani Junior **13**:16-18.

Dallinger, R., B. Berger, R. Triebskorn-Köhler, and H. Köhler. 2001. Soil biology and ecotoxicology. Pages 489–525 *in* G. M. Barker, editor. The biology of terrestrial molluscs. CABI Publishing, Wallingford.

Davis, S. E., III, D. L. Childers, and G. B. Noe. 2006. The contribution of leaching to the rapid release of nutrients and carbon in the early decay of wetland vegetation. Hydrobiologia **569**:87-97.

Dillon, R. T. 2004. The ecology of freshwater molluscs. Cambridge University Press, Cambridge.

Ehrenfeld, J. G. 2010. Ecosystem Consequences of Biological Invasions. Annual Review of Ecology, Evolution, and Systematics **41**:59-80.

Estebenet, A. L. 1995. Food and feeding in *Pomacea canaliculata* (Gastropoda: Ampullariidae). The Veliger **38**:277-283.

Evans, M. A. 2012. Impacts of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) as leaf litter decomposers. University of California Davis.

Fairhurst, T., C. Witt, R. Buresh, and A. Dobermann. 2007. Rice: A practical guide to nutrient management. 2nd edition edition. International Rice Research Institute, International Plant Nutrition Institute, and International Potash Institute.

Hanafi, E. M., H. H. El Khadrawy, W. M. Ahmed, and M. M. Zaabal. 2012. Some observations on rice straw with emphasis on updates of its management. World Applied Sciences Journal **16**:354-361.

Horgan, F. G., A. M. Stuart, and E. P. Kudavidanage. 2012. Impact of invasive apple snails on the functioning and services of natural and managed wetlands. Acta Oecologica **Published online**.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal **50**:346-363.

Ibrahima, A., R. Joffre, and D. Gillon. 1995. Changes in Litter during the Initial Leaching Phase - an Experiment on the Leaf-Litter of Mediterranean Species. Soil Biology & Biochemistry **27**:931-939.

Jenkins, B. M., R. R. Bakker, and J. B. Wei. 1996. On the properties of washed straw. Biomass and Bioenergy **10**:177-200.

Joshi, R. C., E. C. Martin, T. Wada, and L. S. Sebastian. 2006. Role of golden apple snails in organic rice cultivation and weed management. Pages 483-488 *in* R. C. Joshi and L. S. Sebastian, editors. Global advances in ecology and management of golden apple snails. Philippine Rice Research Institute, Nueva Ecija.

Joshi, R. C., and L. S. Sebastian. 2006. Global advances in ecology and management of golden apple snails. Philippine Rice Research Institute, Munoz.

Klotzbücher, T., A. Marxen, D. Vetterlein, J. Schneiker, M. Türke, N. van Sinh, N. H. Manh, H. van Chien, L. Marquez, S. Villareal, J. V. Bustamante, and R. Jahn. 2015. Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. Basic and Applied Ecology.

Koegel-Knabner, I., W. Amelung, Z. Cao, S. Fiedler, P. Frenzel, R. Jahn, K. Kalbitz, A. Koelbl, and M. Schloter. 2010. Biogeochemistry of paddy soils. Geoderma **157**:1-14.

Kuehn, K. A., and K. Suberkropp. 1998. Decomposition of standing litter of the freshwater emergent macrophyte *Juncus effusus*. Freshwater Biology **40**:717-727.

Kurihara, Y. 1989. Ecology of Some Ricefields in Japan as Exemplified by Some Benthic Fauna, with Notes on Management. Internationale Revue der Gesamten Hydrobiologie **74**:507-548.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2015. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-25.

Lach, L., D. K. Britton, R. J. Rundell, and R. H. Cowie. 2000. Food preference and reproductive plasticity in an invasive freshwater snail. Biological Invasions **2**:279–288.

Lekha, A., G. Chopra, and S. R. Gupta. 1989. Role of soil fauna in decomposition of rice and sorghum straw. Proceedings of the Indian Academy of Sciences **98**:275-284.

Litsinger, J. A., and D. B. Estano. 1993. Management of the golden apple snail *Pomacea canaliculata* (Lamarck) in rice. Crop Protection **12**:363-370.

López van Oosterom, M. V., C. S. Ocón, F. Brancolini, M. E. Maroñas, E. D. Sendra, and A. Rodrigues Capítulo. 2013. Trophic relationships between macroinvertebrates and fish in a pampean lowland stream (Argentina). Iheringia. Série Zoologia **103**:57-65.

Lu, Y. H., A. Watanabe, and M. Kimura. 2003. Carbon dynamics of rhizodeposits, root- and shoot-residues in a rice soil. Soil Biology & Biochemistry **35**:1223-1230.

Mulholland, P. J., J. W. Elwood, J. D. Newbold, and L. A. Ferren. 1985. Effect of a leaf-shredding invertebrate on organic-matter dynamics and phosphorus spiraling in heterotrophic laboratory streams. Oecologia **66**:199-206.

Nentwig, W. 2007. Biological Invasions: why it Matters. Springer-Verlag, Berlin Heidelberg.

Okuma, M., K. Tanaka, and S. Sudo. 1994. Weed control method using apple snail (Pomacea canaliculata) in paddy fields. Weed Research **39**:114-119.

Proffitt, C. E., and D. J. Devlin. 2005. Grazing by the intertidal gastropod Melampus coffeus greatly increases mangrove leaf litter degradation rates. Marine Ecology Progress Series **296**:209-218.

Qiu, J.-W., M. T. Chan, K. L. Kwong, and J. Sun. 2011. Consumption, survival and growth in the invasive freshwater snail *Pomacea canaliculata*: does food freshness matter? . Journal of Molluscan Studies **77**:189-195.

Qiu, J.-W., and K.-L. Kwong. 2009. Effects of macrophytes on feeding and life-history traits of the invasive apple snail *Pomacea canaliculata*. Freshwater Biology **54**:1720-1730.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roger, P. A. 1996. Biology and management of the floodwater ecosystem in ricefields. lnternational Rice Research Institute, Manila.

Samra, J. S., B. Singh, and K. Kumar. 2003. Managing crop residues in the rice-wheat system of the Indo-Gangetic plain.*in* J. K. Ladha, editor. Improving the productivity and sustainability of rice–wheat systems: Issues and impacts. ASA Spec. Publ. 65. ASA, CSSA, and SSSA, Madison, WI.

Schaller, J., and E. Struyf. 2013. Silicon controls microbial decay and nutrient release of grass litter during aquatic decomposition. Hydrobiologia **709**:201-212.

Schmidt, A., H. Auge, R. Brandl, K. L. Heong, S. Hotes, J. Settele, S. Villareal, and M. Schädler. 2015. Small-scale variability in the contribution of invertebrates to litter decomposition in tropical rice fields. Basic and Applied Ecology.

Singh, Y., B. Singh, and J. Timsina. 2005. Crop residue management for nutrient cycling and improving soil productivity in rice-based cropping systems in the tropics. Advances in Agronomy **85**:269-407.

Slim, F. J., M. A. Hemminga, C. Ochieng, N. T. Jannink, E. C. delaMoriniere, and G. vanderVelde. 1997. Leaf litter removal by the snail *Terebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). Journal of Experimental Marine Biology and Ecology **215**:35-48.

Tanaka, M. O., A. C. A. Ribas, and A. L. T. de Souza. 2006. Macroinvertebrate succession during leaf litter breakdown in a perennial karstic river in Western Brazil. Hydrobiologia **568**:493-498.

Tavares, D. S., R. C. Maia, and C. A. Rocha-Barreira. 2011. Contribution of Melampus coffeus (Gastropoda, Ellobiidae) to leaf litter decomposition in the middle estuary of the Pacoti river, Ceara, Brazil. Iheringia. Série Zoologia **101**:56-60.

Tian, G., L. Brussaard, and B. T. Kang. 1993. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions: effects on soil fauna. Soil Biology & Biochemistry **25**:731-737.

Tian, G., L. Brussaard, and B. T. Kang. 1995. Breakdown of Plant Residues with Contrasting Chemical-Compositions under Humid Tropical Conditions - Effects of Earthworms and Millipedes. Soil Biology & Biochemistry **27**:277-280.

Weber, S., S. Stubner, and R. Conrad. 2001. Bacterial populations colonizing and degrading rice straw in anoxic paddy soil. Applied and Environmental Microbiology **67**:1318-1327.

Wolters, V. 1991. Soil Invertebrates - Effects on Nutrient Turnover and Soil Structure - A Review. Zeitschrift für Pflanzenernährung und Bodenkunde **154**:389-402.

Youens, A. K., and R. L. Burks. 2008. Comparing applesnails with oranges: the need to standardize measuring techniques when studying *Pomacea*. Aquatic Ecology **42**:679-684.

Chapter 6

SYNTHESIS

IMPACT OF FIELD MANAGEMENT ON DETRITIVORES

- NEWLY GAINED KNOWLEDGE -

The three field experiments of this thesis provide insights into the mechanisms and factors which can influence the assemblage of animals as well as the decomposition by invertebrates in rice-based ecosystems. A consistent pattern across all three studies was the significant increase in mass loss of rice straw under the influence of invertebrate decomposers. Thus, I generally conclude that **in flooded rice agriculture invertebrate decomposers are an essential part for the decomposition of rice straw residuals and can be expected to greatly enhance the nutrient supply by compensating the highly retarded microbial decay rates.**

The three experiments further revealed that the abundance of decomposer invertebrates as well as their contribution to the decomposition process depend on different aspects of rice paddy management. Firstly, since many invertebrate species are reliant on terrestrial habitats in certain stages of their life cycle, surrounding structures of paddies were hypothesized to have an influence on their role as decomposers in rice fields. Secondly, management practices like crop residue management, fertilization, water regime and crop rotation can be expected to have important effects on faunal abundances. The results of the series of field experiments in this thesis can be combined in a conceptual scheme of relationships between these factors and their consequences for the decomposition processes in tropical rice fields (Figure 1).

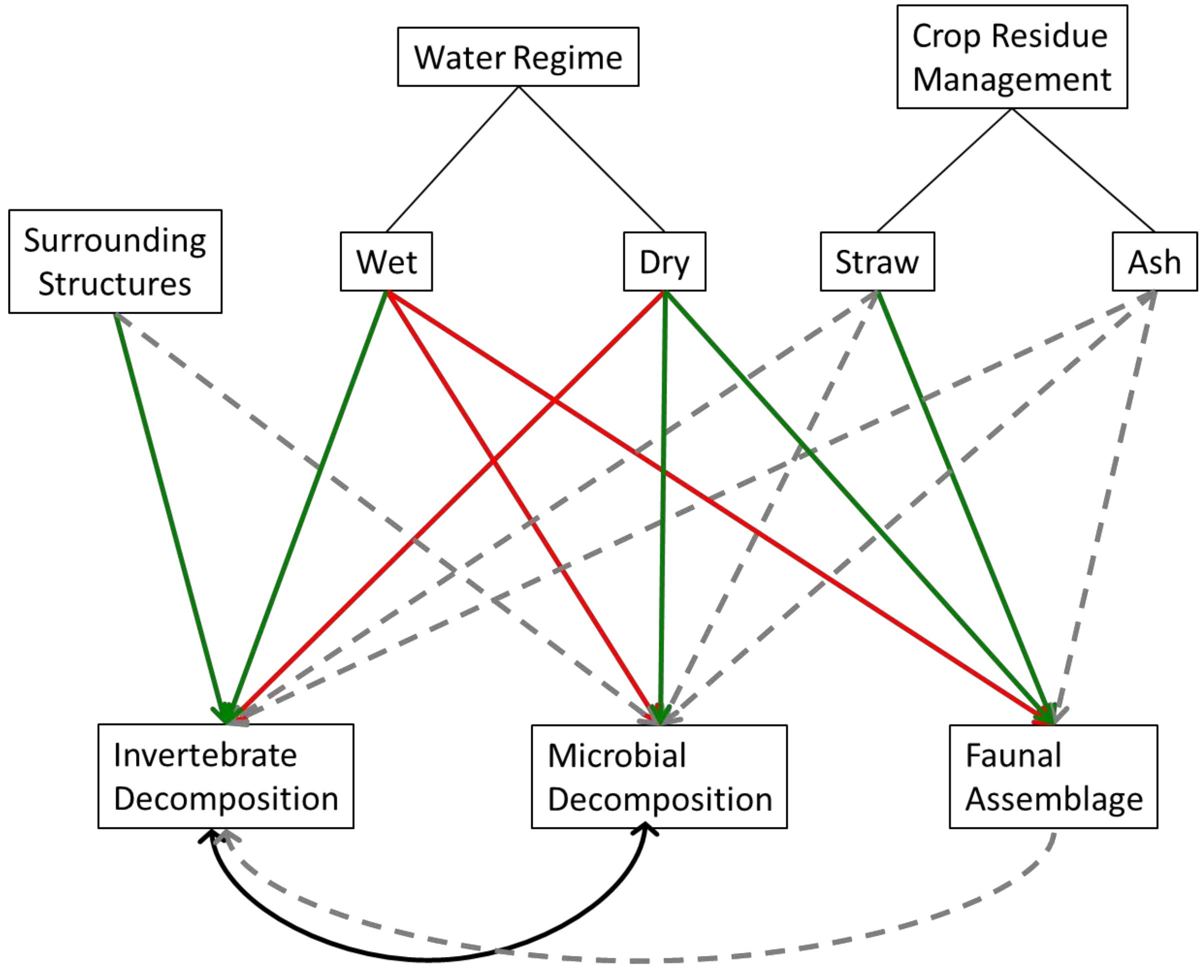

Figure 1 Effects of surrounding structures (Chapter 2), practices of crop residue management (Chapter 3) and crop rotations with altering water regimes (Chapter 4) on decomposition processes and faunal assemblage in rice fields; red arrows indicate a negative effect of the factor on the response variable, green arrows indicate positive effects and grey dashed lines indicate no significant effects; the black double headed arrow indicates an interaction effect.

In Chapter 2 I demonstrated that with decreasing distance to the field border and the adjacent structures the decomposition activity of invertebrate decomposers steadily increased *[Surrounding Structures* → *Invertebrate Decomposition]* while no effect on microbial decomposition rates were detected *[Surrounding Structures* ⇢ *Microbial Decomposition]*. A certain diversity of landscape structures near rice fields is especially important for invertebrates with aquatic larval and terrestrial adult stages including some important decomposer organisms (e.g. chironomids). Similar positive effects of rice field bunds on the activity of invertebrate decomposers were shown by Widyastuti (2002), who concluded that due to the shorter distances to field borders several small fields instead of one big field would enhance decomposition rates and therefore the nutrient supply for plant growth resulting in higher yields.

Crop residues leftover after harvest bear a great potential as natural fertilizer for the next rice cropping season (Singh et al. 2005). Management practices of farmers in this region include (1) burning of straw and spreading the ash on the field, (2) removing the rice straw completely to use it as fodder, or (3) scattering the straw on the field surface or incorporating it into the soil. Rice straw can significantly enhance soil fertility by increasing the content of mineralized N in the soil (Bird et al. 2001, Eagle et al. 2001, Thuy et al. 2008) and therefore decrease the need for artificial fertilizer (Cucu et al. 2014). Rice straw burning results in a loss of these important nutrients (Villegas-Pangga et al. 2000) and is also known to significantly contribute to global warming by the great amounts of methane that get emitted (Houghton 1995, Reicosky et al. 2000, Wassmann et al. 2000). In our experiment rice straw application had particular positive effects on the abundance of meso-invertebrates *[Straw ⟶ Faunal Assemblage]*. However, several crop seasons with continuous residue application are necessary to detect changes in decomposition rates and soil productivity (Singh et al. 2001, Samra et al. 2003, Thuy et al. 2008, Xu et al. 2010). As our study was conducted only during one season, we found no effects on the decomposition rates of invertebrates and microbes *[Straw ⇢ Invertebrate Decomposition/ Microbial Decomposition]*. Nevertheless, our experiment showed that management practices can also have strong short-term effects on faunal groups in rice fields. Studies on the long-term effects of different crop residue management practices are essential for evaluating the benefits of rice straw amendment and its potential for enhancing the sustainability in rice agriculture.

Due to the regular changes in soil moisture from completely flooded during cropping and completely dry in the fallow periods (Bambaradeniya and Amarasinghe 2003) faunal groups of rice fields are specialized on surviving drastic environmental changes. A change in water regime due to the introduction of non-flooded upland crops in the rice cycle increases the length of dry phases which might have negative effects on the community of soil fauna. Crop diversification in rice-based systems also bears the risk of declining the contents of organic matter and nutrients in the soil (Pampolino et al. 2008, Haefele et al. 2013). However, longer dry periods would decrease the extremely high amounts of water consumption and greenhouse gas emissions of irrigated rice cultivation (Bouman et al. 2007, Olk et al. 2007, Mueller et al. 2012). Therefore, we investigated the influences of different crop rotations on the assemblage of soil-dwelling invertebrates and their contribution to rice straw decomposition. During dry phases rice straw decomposition by invertebrate was nearly nonexistent *[Dry ⟶ Invertebrate Decomposition]* while microbial decomposition rates were highly accelerated *[Dry ⟶ Microbial Decomposition]*. In contrast, under flooded conditions decomposition rates of invertebrates were significantly improved *[Wet ⟶ Invertebrate Decomposition]* while microbial decomposition was retarded *[Wet ⟶ Microbial Decomposition]*. We found no differences in the total mass loss of rice straw between the two seasons which supports our hypothesis that invertebrate decomposers can compensate the low microbial decomposition activity under the anaerobic conditions in flooded fields (Canhoto and Graça 1995, Swan and Palmer 2006, Koegel-Knabner et al. 2010, Ferreira et al. 2012). Even though invertebrates were significantly more abundant during dry cropping *[Dry ⟶ Faunal Assemblage]*, they had no detectable influence on the breakdown of rice straw residuals during this time *[Faunal Assemblage* ---> *Invertebrate Decomposition]*. Further, we found no negative effect of the longer dry periods on the activity and abundance of (semi-)aquatic decomposer invertebrates in flooded paddy fields. Nevertheless, it is unknown how crop rotations with different moisture regimes might affect the nutrient supply by rice straw decomposition. Particularly, it has to be evaluated if the increased microbial activity can compensate the ceased impact of invertebrates during the cultivation of dry crops.

KEY RESULTS

- Invertebrate decomposers significantly contribute to rice straw decomposition making them a crucial tool for implementing sustainable agriculture in tropical flooded rice fields, especially as microbial decomposition is retarded under the anoxic conditions prevalent during cropping phases.
- Structural diversity and shorter distances to the bunds positively influence the decomposition activity of invertebrates. Hence, the conversion of the landscape structure into contiguous areas of rice monocultures may reduce the ecosystem services provided by decomposition (e.g. nutrient supply). Farmers should consider using several small fields rather than one big field for rice cropping.
- Practices of crop residue management can significantly influence the assemblage of decomposer animals in the soil and the aquatic phase of flooded rice fields along with its decomposition efficiency. Higher mesofaunal abundances in fields with rice straw amendment compared to fields where the ash of burned straw was applied indicate that recycling the rice straw residuals for fertilization could increase natural nutrient supply.
- Crop rotations including dry upland crops increase the abundance of terrestrial soil faunal groups during dry cropping phases. In these seasons invertebrates had no visual effect on rice straw decomposition, but microbial decomposition rates were highly accelerated. In the wet phases of the crop cycle invertebrate decomposers significantly contributed to rice straw decomposition while microbial decay rates were retarded. These compensatory mechanisms in the decomposition of organic matter by invertebrates and microbes led to similar amounts of mass loss of rice straw residuals between dry and wet phases. The longer dry periods due to the insertion of an upland crop in the dry season did not have any measurable negative effect on the decomposition efficiency of invertebrates during wet rice cropping.
- Some abundant invertebrate groups classified as pests could positively contribute to ecosystem services during times when rice plants are not vulnerable. Golden apple snails were shown to contribute to rice straw decomposition and therefore they could increase the nutrient supply for plant growth. Thus, their negative impact on rice yield due to herbivory is partly alleviated by their involvement in the decomposition process.

CONCLUSION

My thesis provides insights into the composition of aquatic and soil-dwelling animal assemblages in flooded paddy fields and their potential role in nutrient cycling processes. Decomposition is an essential ecosystem service which provides natural supply of nutrients for plant growth and decreases the need for applying artificial fertilizers. In flooded rice ecosystems invertebrates are of particular importance for an efficient decay of organic matter as microbial decomposition is considerably decelerated under anaerobic conditions. The experiments presented in this thesis substantiate the value of invertebrate detritivores for an effective breakdown of crop residues and therefore, for a sufficient nutrient availability in paddy soils. Further, my experiments revealed that the role of invertebrates in decomposition processes has to be seen in the context of field management. Thus, the development of sustainable management practices in rice agro-ecosystems should also be based on the knowledge about the mediating effects of different cultivation methods on decomposition as an ecologically and economically relevant ecosystem function. Continued efforts to reveal the link between the assemblage of animals in rice fields and their role in decomposition processes are crucial to extend our understanding of the mechanisms behind nutrient utilization promoted by rice straw decomposition. Exploiting the full fertilization potential of rice straw residuals will help to establish sustainable methods for productive rice agriculture.

REFERENCES OF CHAPTER 6

Bambaradeniya, C. N. B., and F. P. Amarasinghe. 2003. Biodiversity associated with the rice field agroecosystem in Asian countries: A brief review. Working Paper 63, Colombo, Sri Lanka: International Water Management Institute.

Bird, J. A., W. R. Horwath, A. J. Eagle, and C. van Kessel. 2001. Immobilization of fertilizer nitrogen in rice: Effects of straw management practices. Soil Science Society of America Journal **65**:1143-1152.

Bouman, B. A. M., E. Humphreys, T. P. Tuong, and R. Barker. 2007. Rice and Water. Pages 187-237 *in* L. S. Donald, editor. Advances in Agronomy. Academic Press.

Canhoto, C., and M. A. S. Graça. 1995. Food value of introduced eucalypt leaves for a Mediterranean stream detritivore: Tipula lateralis. Freshwater Biology **34**:209-214.

Cucu, M. A., D. Said-Pullicino, V. Maurino, E. Bonifacio, M. Romani, and L. Celi. 2014. Influence of redox conditions and rice straw incorporation on nitrogen availability in fertilized paddy soils. Biology and fertility of soils **50**:755-764.

Eagle, A. J., J. A. Bird, J. E. Hill, W. R. Horwath, and C. van Kessel. 2001. Nitrogen dynamics and fertilizer use efficiency in rice following straw incorporation and winter flooding. Agronomy Journal **93**:1346-1354.

Ferreira, V., A. C. Encalada, and M. A. S. Graça. 2012. Effects of litter diversity on decomposition and biological colonization of submerged litter in temperate and tropical streams. Freshwater Science **31**:945-962.

Haefele, S. M., N. P. M. Banayo, S. T. Amarante, J. D. L. C. Siopongco, and R. L. Mabesa. 2013. Characteristics and management options for rice–maize systems in the Philippines. Field Crops Research **144**:52-61.

Houghton, R. A. 1995. Changes in the storage of terrestrial carbon since 1850. Pages 45-66 *in* R. Lal, J. Kimball, E. Levine, and B. A. Stewart, editors. Soils and global change. CRC Press, Boca Raton, Florida.

Koegel-Knabner, I., W. Amelung, Z. Cao, S. Fiedler, P. Frenzel, R. Jahn, K. Kalbitz, A. Kölbl, and M. Schloter. 2010. Biogeochemistry of paddy soils. Geoderma **157**:1-14.

Mueller, N. D., J. S. Gerber, M. Johnston, D. K. Ray, N. Ramankutty, and J. A. Foley. 2012. Closing yield gaps through nutrient and water management. Nature **490**:254-257.

Olk, D. C., M. I. Samson, and P. Gapas. 2007. Inhibition of nitrogen mineralization in young humic fractions by anaerobic decomposition of rice crop residues. European Journal of Soil Science **58**:270-281.

Pampolino, M. F., E. V. Laureles, H. C. Gines, and R. J. Buresh. 2008. Soil Carbon and Nitrogen Changes in Long-Term Continuous Lowland Rice Cropping. Soil Science Society of America Journal **72**:798-807.

Reicosky, D. C., J. L. Hatfield, and R. L. Sass. 2000. Agricultural contributions to greenhouse gas emissions. Pages 37-55 *in* M. V. Reddy and H. F. Hodges, editors. Climate Change and Global Crop Productivity. CABI Publishing, Wallingford, UK.

Samra, J. S., B. Singh, and K. Kumar. 2003. Managing crop residues in the rice-wheat system of the Indo-Gangetic plain.*in* J. K. Ladha, editor. Improving the productivity and sustainability of rice–wheat systems: Issues and impacts. ASA Spec. Publ. 65. ASA, CSSA, and SSSA, Madison, WI.

Singh, B., K. F. Bronson, Y. Singh, T. S. Khera, and E. Pasuquin. 2001. Nitrogen-15 balance as affected by rice straw management in a rice–wheat rotation in northwest India. Nutrient Cycling in Agroecosystems **59**:227-237.

Singh, Y., B. Singh, and J. Timsina. 2005. Crop residue management for nutrient cycling and improving soil productivity in rice-based cropping systems in the tropics. Advances in Agronomy **85**:269-407.

Swan, C. M., and M. A. Palmer. 2006. Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. Oecologia **147**:469-478.

Thuy, N. H., Y. Shan, B. Singh, K. Wang, Z. Cai, Y. Singh, and R. J. Buresh. 2008. Nitrogen Supply in Rice-Based Cropping Systems as Affected by Crop Residue Management. Soil Sci. Soc. Am. J. **72**:514-523.

Villegas-Pangga, G., G. Blair, and R. Lefroy. 2000. Measurement of decomposition and associated nutrient release from straw (Oryza sativa L.) of different rice varieties using a perfusion system. Plant and Soil **223**:1-11.

Wassmann, R., H. U. Neue, R. S. Lantin, K. Makarim, N. Chareonsilp, L. V. Buendia, and H. Rennenberg. 2000. Characterization of Methane Emissions from Rice Fields in Asia. II. Differences among Irrigated, Rainfed, and Deepwater Rice. Nutrient Cycling in Agroecosystems **58**:13-22.

Widyastuti, R. 2002. Soil fauna in rainfed paddy field ecosystems: their role in organic matter decomposition and nitrogen mineralization. Ecology and Development Series Band 3. Cuvillier Verlag, Göttingen.

Xu, Y., L. Nie, R. J. Buresh, J. Huang, K. Cui, B. Xu, W. Gong, and S. Peng. 2010. Agronomic performance of late-season rice under different tillage, straw, and nitrogen management. Field Crops Research **115**:79-84.

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Appendix

EIGENSTÄNDIGKEITSERKLÄRUNG

Ich versichere, dass ich meine Dissertation

“Decomposition driven by invertebrates in tropical rice ecosystems: impacts of management strategies”

selbstständig, ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe. Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle/Saale, 05.08.2015

Anja Schmidt